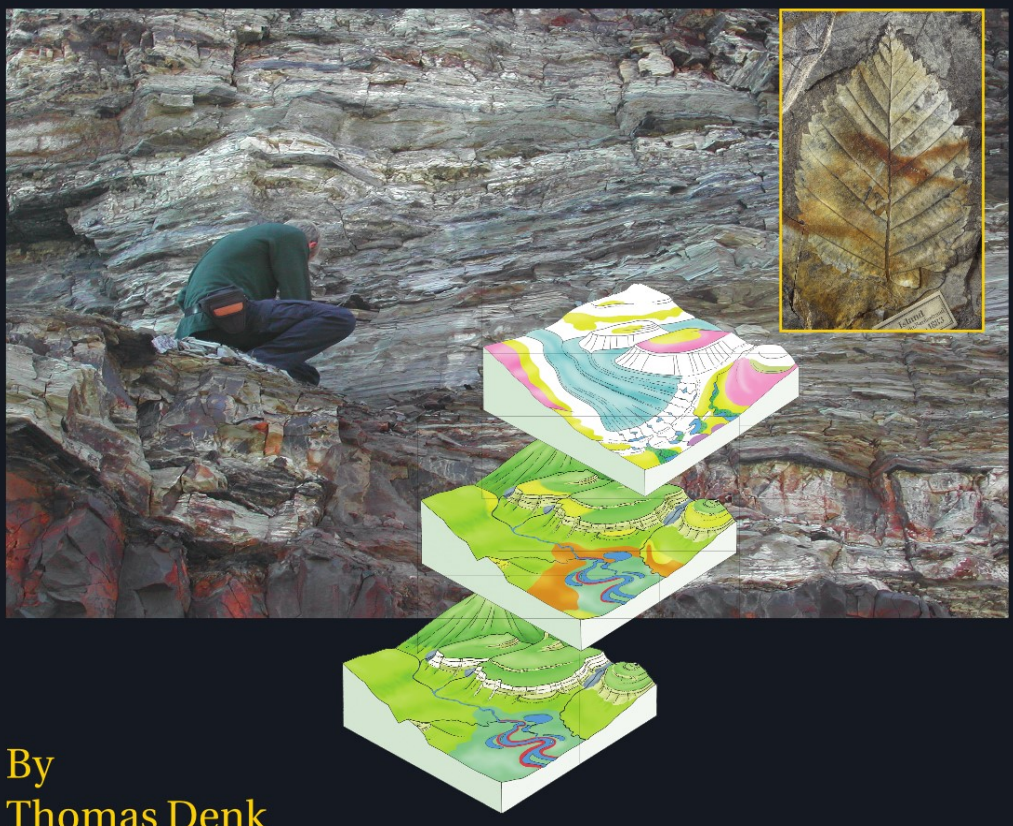


Volume 35 TOPICS IN GEOBIOLOGY Series Editors: Neil H. Landman and Peter J. Harries

# Late Cainozoic Floras of Iceland

## 15 Million Years of Vegetation and Climate History in the Northern North Atlantic



By
Thomas Denk
Friðgeir Grímsson
Reinhard Zetter
Leifur A. Símonarson

Springer

# Late Cainozoic Floras of Iceland

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## 15 Million Years of Vegetation and Climate History in the Northern North Atlantic

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Springer

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*Cover illustrations*:
Main photo: Studying sediments at Surtarbrandsgil-Brjánslækur, photo by Gerwin F. Gruber
Insert photo: *Betula islandica*, photo by T. Denk
Insert drawings: Schematic block diagrams showing palaeo-landscape and vegetation types for Pleistocene interglacials, the early Late Miocene and the Middle Miocene of Iceland, drawings by N. Frotzler and P. von Knorring
Top row photos: from left to right, SEM micrographs of pollen grains of *Tilia* from Botn, Apiaceae, Asteraceae, and *Pinus* from Tröllatunga, *Viscum* from Tjörnes, and *Salix* from Tröllatunga. Photos by Reinhard Zetter and Friðgeir Grímsson.

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*It is only by combing the information furnished by all the earth sciences that we can hope to determine "truth" here, that is to say, to find the picture that sets out all the known facts in the best arrangements and that therefore has the highest degree of probability. Further, we have to be prepared always for the possibility that each new discovery, no matter which science furnishes it, may modify the conclusions we draw.*

Alfred Wegener, *The Origins of Continents and Oceans, 4th edition, 1970, p. XXX*
[University Paperbacks, John Dickens & Co. Ltd., Northampton, 251 pp.]

*Nur durch Zusammenfassung aller Geo-Wissenschaften dürfen wir hoffen, die „Wahrheit" zu ermitteln, d. h. dasjenige Bild zu finden, das die Gesamtheit der bekannten Tatsachen in der besten Ordnung darstellt und deshalb den Anspruch auf größte Wahrscheinlichkeit hat; und auch dann müssen wir ständig darauf gefaßt sein, daß jede neue Entdeckung, aus welcher Wissenschaft immer sie hervorgehen möge, das Ergebnis modifizieren kann.*

Alfred Wegener, *Die Entstehung der Kontinente und Ozeane, 4. umgearbeitete Auflage, 1929, p. X*
[Friedrich Vieweg & Sohn, Braunschweig, 231 pp.]

# Foreword

All fossil deposits serve as time machines, capturing the biota of a particular point in the past history of the planet. But often they are static, being but a single point in the moving path of history. With the *Late Cainozoic Floras of Iceland*, Thomas Denk, Friðgeir Grímsson, Reinhard Zetter and Leifur A. Símonarson have assembled detailed information using a range of organs to catalogue a superimposed series of floras, providing a dynamic view of changing biota in one place through time. This is, in its own right, an outstanding contribution that parallels other regional summations (e.g., Dorofeev, 1963; Tanai, 1972; Mai, 1995). However, the current volume has a further value.

Iceland is not simply a geographically isolated sample of flora through time, but is a sample of a flora at a crossroads between the Old World and the New – it sits as a toll booth of history, collecting record of the passage of plants across the northern North Atlantic for the last 15 million years. Not until Greenland becomes sufficiently de-glaciated to tell its story (and possibly not even then if the glaciers have removed the evidence) will we know more about the passage of species, and thus floras, in the exchange that developed the links that exist between western Europe and North America in the later Tertiary, Quaternary and into the present.

The data are ripe for the taking. Known since the middle of the nineteenth century (Heer, 1859, 1868) it has required more than 150 years to arrive at this full compendium, a synthesis first essayed by Akhmetiev et al. in 1978. To realize this, the authors have revisited both museum specimens and field sites to assemble a range of foliar and pollen materials which have then been analyzed using the most recent methodologies. From this they recognize ca 36 Miocene, 3 Pliocene and 6 Pleistocene floras covering a range from warm-temperate, mixed mesophytic vegetation to the modern flora of the island.

Using these data, the authors have reconstructed the changing vegetation and climate of Iceland and carefully tracked the appearance and disappearance of biogeographically important taxa, permitting inference of both the timing, and in some cases, direction of migration of lineages between the Old and New Worlds. What is immediately apparent is that the North Atlantic Land Bridge was viable until much more recently than earlier authors (e.g., Tiffney, 1985) had surmised. While global cooling reduced the diversity of taxa, increasingly limiting it to cool-temperate

lineages, these were still in motion and contributed to shared elements of the modern floras of western Europe and North America. These are new and important contributions to our ever-expanding knowledge of the floristic dynamics of the Northern Hemisphere.

Santa Barbara — Bruce H. Tiffney
Gainesville — Steven R. Manchester

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# Chapter 1
# Introduction to the Nature and Geology of Iceland

*Travelling in the interior of Iceland is very arduous work, for the country lies high and consists for the most part of sand and lava deserts, often absolutely without grass. The traveller has consequently to take with him even fodder for the horses. The summer, moreover, is short, and the route into the interior occupies much time.*

Dr. Thoroddsen's explorations in Iceland, Anonymous 1893

**Abstract** Iceland is an island in the northern North Atlantic halfway between Europe and Greenland/North America and some of its northern parts touch the Arctic Circle. Its position at the conjunction of warm southerly and cold northerly waters and air masses contribute to a particular climate that is unusually mild considering the high latitude of the island. From a biogeographical point of view, Iceland is an important place for both palaeontologists and recent botanists and zoologists. Geologically, Iceland is unique as it is situated at the boundary of the North American and Eurasian plates and is one of the few places on the Earth where sea-floor spreading can be witnessed on land. In this northern part of the Atlantic, the North American continent began to move away from the Eurasian continent by rifting and sea-floor spreading in the early Palaeogene, ca 55 Ma. When sea-floor spreading initiated in this area, a rich flow of magma generated by a mantle plume caused thermal doming of the crust and formed a connection or 'land bridge' between the continents known as the Greenland-Scotland Transverse Ridge. Subsequently, the eastern and western limits of this bridge sank as a consequence of continuous rifting and crustal cooling. Today, Iceland is still subaerial because of its position over this very same mantle plume. In the late Cainozoic, rift relocation had an important effect on the geology of Iceland and caused massive erosion and deposition of sediments, some of which contain the plant fossils described in this book. This chapter provides an introduction to the recent climate, weather systems and ocean currents affecting Iceland, and presents the most important details of the island's living fauna and flora. We also outline the geological background necessary to place the fossiliferous formations in a context.

T. Denk et al., *Late Cainozoic Floras of Iceland*, Topics in Geobiology 35,
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## 1.1 Geographic Position

Iceland is the second largest island in Europe, after Great Britain, with a total area of 103,100 km$^2$, the mainland comprising 102,950 km$^2$ (Fig. 1.1). The island lies between longitudes 13°29.6′W and 24°32.1′W and between latitudes 63°23.4′N



**Fig. 1.1** A MODIS satellite image of Iceland, taken on NASA's Aqua satellite on August 11, 2004. Part of Greenland can bee seen NW and the Faeroe Islands SE (top right) of Iceland (Image courtesy of MODIS Rapid Response project at NASA/GSFC, http://modis.gsfc.nasa.gov/)

and 66°32.3′N, with the northernmost parts touching the Arctic Circle. Outside these limits are the skerries of Kolbeinsey and Hvalbakur, and also some of the Vestmannaeyjar (Westman Islands). The southernmost of the Vestmannaeyjar is the newborn island of Surtsey, which rose from the sea during a submarine eruption in 1963. The shortest distance to Greenland is ca 280 km, to the Faeroe Islands ca 435 km, to Scotland ca 790 km, and to Norway ca 970 km. Thus, Iceland has a unique and biogeographically important position in the northern North Atlantic, midway between North America and Europe, and at the boundary between the Arctic and Boreal regions.

## 1.2 Climate and Ocean Currents

### *1.2.1 Climate*

The Icelandic climate is influenced by various air masses, some of which originate in polar regions while others have a tropical origin (Einarsson 1976). The interaction between warm southerly and cold northerly ocean currents and air masses affects both the course and the frequency of the weather systems around Iceland and is the cause of its typical instability. Einarsson (1984) described the main weather systems relevant to Iceland. Depending on the track and position of low and high pressure zones in and adjacent to Iceland (Greenland, British Isles, and Scandinavia), weather systems such as "Southern with warm air masses" or "Northern" bring humid or dry and cold or warm air masses from different directions. The "Southern with warm air masses", for instance, is active when a low pressure zone over southern Greenland and an anticyclone over Western Europe cause tropical air masses to flow northwards, towards Iceland (Einarsson 1984). Since Iceland is mountainous, precipitation and cloudiness increase windward of the mountains and decrease leeward.

The climate is considerably warmer than might be expected, considering how far north Iceland lies. During the years 1878–2002 the mean annual temperature in Reykjavík, situated on the southwest coast, was 4.3°C, with −0.6°C as the mean temperature in January, the coldest month, and 10.8°C in July, the warmest month (Hanna et al. 2004). In northern Iceland, the mean annual temperature during these years was 2.3°C on the island of Grímsey, with −1.3°C and 7.7°C, respectively for the coldest and warmest months (Hanna et al. 2004). The lowest temperature measured in Iceland was −37.9°C at Grímsstaðir á Fjöllum in northeastern Iceland, in January 1918, and the highest temperature was 30.6°C at Teigarhorn in eastern Iceland, in June 1939 (Eythorsson and Sigtryggsson 1971).

In the years 1931–1960, the mean annual precipitation was 805 mm at Reykjavík (90 mm in January, 48 mm in July), 474 mm at Akureyri (45 mm in January and 35 mm in July) and 2,256 mm at Vík in Mýrdalur on the south coast (182 mm in January and 169 mm in July; Eythorsson and Sigtryggsson 1971). The true precipitation may have been higher, because the amount of snowfall is difficult to quantify, particularly when it occurs during stormy weather (Rögnvaldsson et al. 2004).

The highest precipitation is in the southeast with estimated maximum annual values of more than 4,000 mm on the ice caps Vatnajökull and Mýrdalsjökull, whereas in the highlands north of Vatnajökull the mean value for the years 1931–1960 was less than 400 mm (Einarsson 1976). Snow cover as a percentage of total surface area for every day in October to May in the years 1931–1960 was 17% in Fagurhólsmýri, on the south coast, 32% in Reykjavík, 53% in Húsavík on the north coast, and 70% on Suðureyri in northwestern Iceland (Einarsson 1976).

In general, the climate of Iceland can be categorized as cold-temperate oceanic. The climate is temperate and humid, with cool and short summers (Cfc climate; Köppen and Geiger 1928; Köppen 1936; Kottek et al. 2006) in the southern and western parts of the country as well as the inner parts (fjords) of northern and eastern Iceland. Here, the mean temperature of the warmest month is ca 10°C and of the coldest month >−3°C. In contrast, the climate is arctic (ET, sensu Köppen 1936; Kottek et al. 2006) on peninsulas and promontories in northwestern, northern and eastern Iceland as well as in the highlands, where the warmest month mean temperature is <10°C (Einarsson 1984).

During the last century, there has been a slight climatic amelioration (Hanna et al. 2004; Fig. 1.2a). The warming was non-uniform in time, with three distinct phases; approximately from 1880 to 1900, from 1925 to 1940, and from 1983 onwards. Warming was most rapid during the second phase, reaching the maximum value over the entire record in 1939 and 1941 (Hanna et al. 2004). This gradual increase in temperature was not accompanied by a shift in mean annual precipitation, which has remained essentially constant between 1881 and 2001 (Hanna et al. 2004; Fig. 1.2b).

Glaciers in Iceland result from special climatic conditions (Fig. 1.3), of which temperature and precipitation, mainly as snowfall, are the most important. During the Pleistocene cold phases, glaciers affected environmental conditions in Iceland. During the Last Glacial Maximum at ca 20 ka BP, glaciers extended towards the shelf break around Iceland. Ice-free enclaves occurred in a few high coastal mountains (Norðdahl et al. 2008). Although glaciers have greatly declined in size since then, their fluctuations are a good indicator of subtle climatic changes. After the 1890s, a general recession of glaciers in Iceland started, and this became quite rapid after 1930. However, cooler summers occurred after 1940 and glaciers retreated more slowly after the 1960s, with steep glaciers starting to advance around 1970. Since 1985, the climate has once more started to warm, and this has steadily led to a more widespread glacial retreat (cf. Björnsson and Pálsson 2008; Fig. 1.2a).

### *1.2.2 Ocean Currents*

The climate of Iceland is strongly affected by the conflux of two ocean currents with very different characteristics: the cold, southwards flowing euhaline East Greenland Current and the warm, saline northwards flowing North Atlantic Current, a continuation of the Gulf Stream. This pattern of ocean currents is one of the key climatic factors in the North Atlantic and adjacent land masses and a clear relationship has been demonstrated between air and sea surface temperatures around Iceland (Stefánsson 1991).

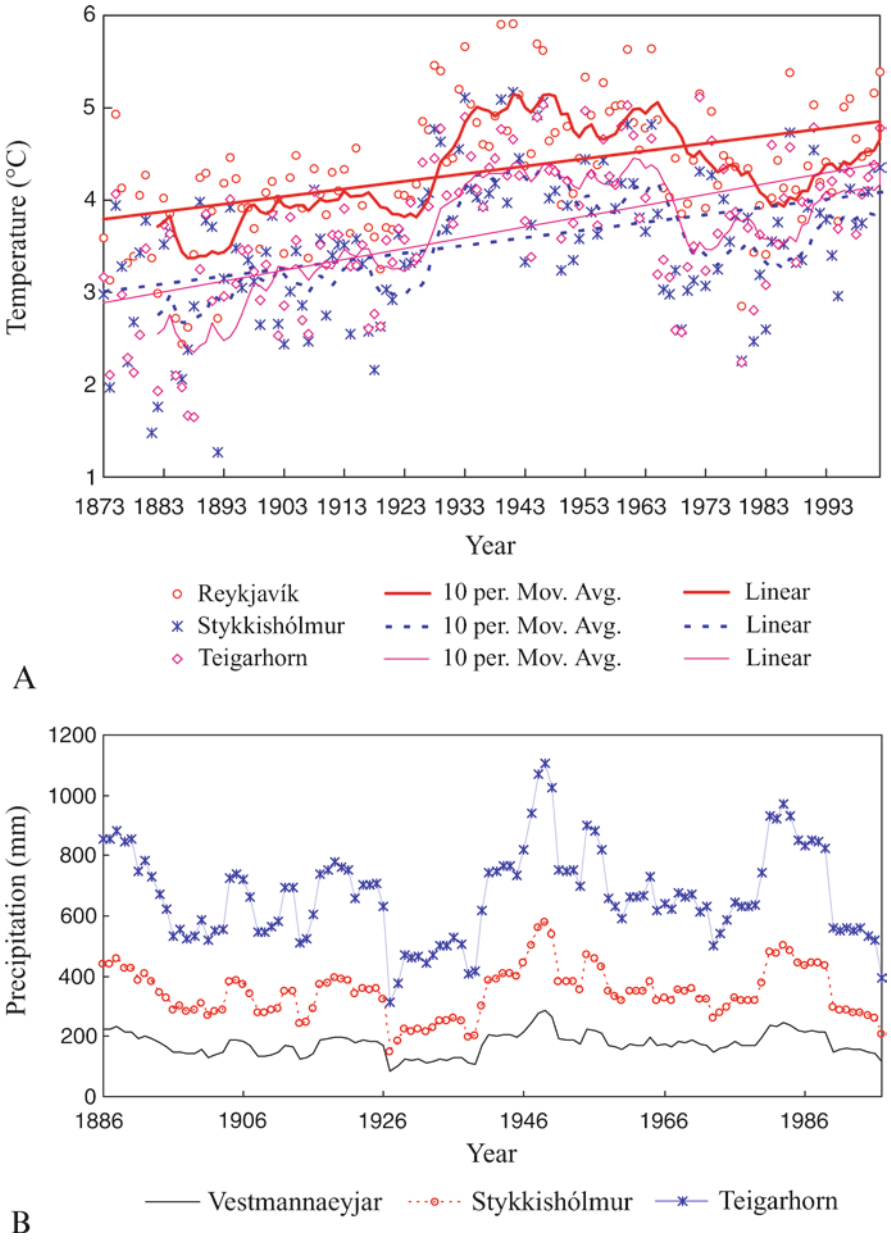



**Fig. 1.2** Recent development of mean annual temperature **(a)**, and mean annual precipitation **(b)**, in Iceland (Modified after Hanna et al. 2004)

The main oceanic circulation pattern around Iceland was probably established when the final closure of the Central American Seaway at 4.6–3.6 Ma led to a flow of surface water from the Pacific Ocean into the Arctic Ocean, via the Bering Strait (Backman 1979; Haug and Tiedemann 1998; Marincovich 2000; Símonarson and



**Fig. 1.3** The meltwater lake Jökulsárlón, southeastern Iceland, with floating icebergs in front of a retreating glacier. Note the outlet glaciers visible behind the lake that are running from the large Breiðamerkurjökull glacier (part of Vatnajökull icecap) in the background

Eiríksson 2008). Due to the presence of a submarine ridge (Iceland-Faeroe Ridge, part of the Greenland-Scotland Transverse Ridge) lying between Iceland and the Faeroe Islands, the North Atlantic Current is deflected westwards and forms the Irminger Current that flows clockwise around the south and west coasts of Iceland (Fig. 1.4). Another branch of the North Atlantic Current, the Norwegian Atlantic Current, continues northwards to the Norwegian-Greenland Seas (Fig. 1.4), where it ultimately sinks and forms the dense North Atlantic Deep Water that flows back southwards, past the east side of Iceland, towards the equator.

The cold euhaline East Icelandic Current is a southeast flowing branch of the East Greenland Current that meets warmer Atlantic waters off the northeast coast of Iceland, at the polar front (PF; Fig. 1.4). The cold period of 1965–1971 (Fig. 1.2a) was caused when the East Icelandic Current was mixed with the warmer Irminger Current, north of Iceland (Stefánsson 1994). This weakened the influence of the latter towards the east, along the north coast of Iceland, so that it almost completely died out off the northeast and east coasts. As a result, temperatures in Iceland dropped markedly. Another effect of the changing interplay of these two currents was that a considerable amount of arctic drift-ice came to the northwestern, northern, and eastern coasts of Iceland, a further cause of the decreased temperatures at that time (Stefánsson 1994).

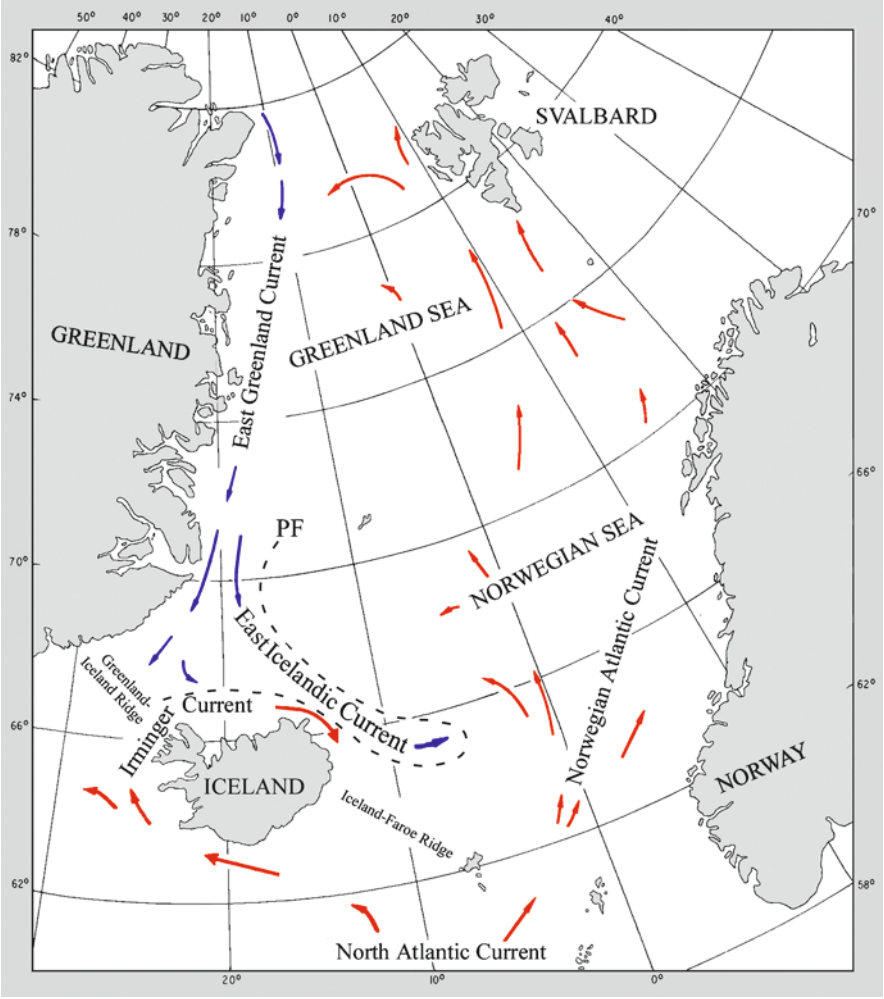



**Fig. 1.4** Map of the northern North Atlantic showing the main oceanic currents around Iceland (Modified after Hurdle 1986; Eiríksson et al. 1992)

## 1.3 Flora and Vegetation

The modern biota of Iceland is characterized by a remarkably low number of endemic plants and animals (cf. Brochmann et al. 2003; Ægisdóttir and Þórhallsdóttir 2004). Apart from the apomictic genera *Alchemilla, Taraxacum* and *Hieracium*, endemic plants in Iceland are restricted to taxa below the species rank.

At present, about 460 vascular plants have been found in Iceland (Table 1.1), the vast majority of which are of European origin (Einarsson 1963). Of these species, ca 40 are ferns and fern allies, but only one native conifer species exists (*Juniperus communis* L.).

**Table 1.1** Plant families and number of genera found in the Icelandic flora. The number of woody plants is indicated (List based on Löve 1945, 1977; Stefánsson 1948; Bjarnason 1983; Kristinsson 1998)

| Family[a] | Genera | Species |
|---|---|---|
| Lycopdiales | | |
| Isoetaceae | 1 | 2 |
| Lycopodiaceae | 3 | 5 |
| Selaginellaceae | 1 | 1 |
| Equisetales | | |
| Equisetaceae | 1 | 7 |
| Polypodiales | | |
| Adiantaceae | 1 | 1 |
| Aspleniaceae | 1 | 3 |
| Blechnaceae | 1 | 2 |
| Dryopteridaceae | 2 | 3 |
| Hymenophyllaceae | 1 | 1 |
| Ophioglossaceae | 2 | 6 |
| Polypodiaceae | 1 | 1 |
| Thelypteridaceae | 1 | 1 |
| Woodsiaceae | 4 | 6 |
| Coniferales | | |
| **Cupressaceae** | **1** | **1** |
| Angiosperms, Monocots | | |
| Alliaceae | 1 | 1 |
| Cyperaceae | 5 | 53 |
| Juncaceae | 2 | 20 |
| Juncaginaceae | 1 | 2 |
| Orchidaceae | 6 | 7 |
| Poaceae | 27 | 47 |
| Potamogetonaceae | 2 | 8 |
| Sparganiaceae | 1 | 3 |
| Tofieldiaceae | 1 | 1 |
| Trilliaceae | 1 | 1 |
| Zannichelliaceae | 1 | 1 |
| Zosteraceae | 1 | 1 |
| Angiosperms, Eudicots (Tricolpates) | | |
| Apiaceae | 4 | 5 |
| Araliaceae | 1 | 1 |
| Asteraceae | 19 | 25 |
| **Betulaceae** | **1** | **2** |
| Boraginaceae | 2 | 5 |
| Brassicaceae | 10 | 21 |
| Callitrichaceae | 1 | 5 |
| Campanulaceae | 1 | 2 |
| Caryophyllaceae | 10 | 27 |
| Chenopodiaceae | 2 | 4 |
| Cornaceae | 1 | 1 |
| Crassulaceae | 3 | 5 |
| Diapensiaceae | 1 | 1 |
| Dipsacaceae | 2 | 2 |
| Droseraceae | 1 | 1 |
| **Empetraceae** | **1** | **1** |
| **Ericaceae** | **9** | **11** |
| Fabaceae | 5 | 11 |
| Gentianaceae | 5 | 7 |
| Geraniaceae | 1 | 1 |
| Haloragaceae | 1 | 2 |
| Hippuridaceae | 1 | 2 |
| Lamiaceae | 3 | 3 |
| Lentibulariaceae | 2 | 2 |
| Linaceae | 1 | 1 |
| Menyanthaceae | 1 | 1 |
| Onagraceae | 2 | 9 |
| Oxalidaceae | 1 | 1 |
| Papaveraceae | 1 | 1 |
| Plantaginaceae | 2 | 4 |
| Parnassiaceae | 1 | 1 |
| Plumbaginaceae | 1 | 1 |
| Polemoniaceae | 1 | 1 |
| Polygonaceae | 5 | 10 |
| Portulacaceae | 1 | 1 |
| Primulaceae | 3 | 4 |
| Pyrolaceae | 2 | 3 |
| Ranunculaceae | 5 | 10 |
| **Rosaceae** | **13** | **26** |
| Rubiaceae | 1 | 6 |
| **Salicaceae** | **2** | **5** |
| Saxifragaceae | 1 | 15 |
| Scrophulariaceae | 7 | 20 |
| Urticaceae | 1 | 2 |
| Valerianaceae | 1 | 1 |
| Violaceae | 1 | 5 |
| Total | 211 | 460 |

[a]Boldface indicates a woody habit of at least some Icelandic members of this family

A further ca 275 species are angiosperms, of which ca 145 species are monocotyledons (Löve 1945, 1977; Stefánsson 1948; Bjarnason 1983; Kristinsson 1998). The most species-rich families are the monocot families Cyperaceae and Poaceae (Table 1.1). The Caryophyllaceae and Asteraceae are the most diverse families among the remaining angiosperms.

The only tree that forms woodlands is *Betula pubescens* Ehr., which can grow up to 10–12 m tall (Blöndal 1987; Fig. 1.5). Scattered within birch woods are solitary trees of *Sorbus aucuparia* L., which can also grow up to 12 m high. A few isolated stands of *Populus tremula* L. exist, mainly in the northeastern part of the island. One species of *Salix* (*S. phylicifolia* L.) is a typical element of birch woods, mostly as a shrub, but sometimes attaining tree stature (Blöndal 1987).

The bryophyte flora of Iceland includes ca 600 species (Jóhannsson 2003) and ca 735 species of lichens are known (Kristinsson 2009). Fungi comprise ca 2,000 species (Kristinsson 2009). Furthermore, about 1,500 species of algae have been reported in Icelandic waters (Kristinsson 2009).

About 97% of the vascular plants native to Iceland have also been recorded in Norway and about 86% in the British Isles. In contrast, only 64% are also found in Greenland (Einarsson 1963, 1975). The western elements in the Icelandic flora, i.e. plants with their main distribution area in the west of Iceland, are very few in number; only ten species of vascular plants belong to this group (Einarsson 1975). About 33% of the vascular plants in Iceland are arctic-alpine disjuncts while the others are boreal (Einarsson 1975).



**Fig. 1.5** A small tree of *Betula pubescens* standing out from the surrounding vegetation made up of willow and heath in Þingvellir national park, southwestern Iceland

### *1.3.1 Development of Modern Vegetation*

The origin of biota located in formerly glaciated areas, such as Iceland, has been a matter of considerable debate. Two main hypotheses have been put forward. The 'nunatak hypothesis'(Blytt 1876; Sernander 1896) suggests that plants survived during glaciations on mountain tops whilst the '*tabula rasa* hypothesis' (Nathorst 1892) proposes total elimination of vascular plants in glaciated areas.

Rundgren and Ingólfsson (1999) used a pollen profile from northern Iceland spanning the period 11.3–9.0 ka to suggest that at least some plant taxa survived the Younger Dryas glacial between 11.0 and 10.0 ka, *in situ,* in ice-free places of Iceland. From this, they concluded that these taxa might also have survived the whole Weichselian cold phase on the island. However, the larger part of the modern flora appears to have reached Iceland from Europe and northern Eurasia, via long-distance dispersal. A continuous long-distance influx of seeds and vegetative parts by ocean currents (in sea water or on drift-ice) and by wind and birds, in both the Holocene and earlier epochs, has been suggested as an explanation for the lack of endemics in Iceland (for references see Rundgren and Ingólfsson 1999). Repeated long-distance dispersal by wind and drifting sea-ice has also been suggested to have facilitated the colonization of Arctic islands after the Pleistocene glaciations by a number of phylogeographic studies. For nine plant species, Alsos et al. (2007) showed that repeated colonization of Svalbard has occurred, from all possible adjacent source areas. Gabrielsen et al. (1997) and Abbott et al. (2000), based on a review of the fossil record of the Arctic-Alpine disjunct species *Saxifraga oppositifolia* L. and molecular data, found clear evidence for a post-glacial colonization of high latitude areas that were covered by ice, by southern periglacial populations. These studies, and the comprehensive review by Brochmann et al. (2003), provide good evidence for recent (post-glacial) migration of many plant and animal taxa across the Atlantic.

When Iceland was first settled in the ninth century, no herbivorous mammals were living on the island and most of the lowlands were covered by birch woods and scrubs. Sigurðsson (1977) estimated that at least 25–30% of the island was covered by birch woods, and 65% of the island was covered by vegetation. After the settlement, woods were cut down for fuel and building purposes and were also heavily grazed by sheep. Hence, wood- and scrublands were gradually destroyed and soil erosion started (Thorarinsson 1944). As a consequence, the present-day vegetation cover amounts only to ca 25% of the country's area (Blöndal and Thorsteinsson 1986).

## 1.4 Fauna on Land and in Adjacent Waters

Iceland has very few native terrestrial mammals. At the time of settlement, the Arctic Fox (*Alopex lagopus* L.; Fig. 1.6) was the only living land mammal and it is still common (Hersteinsson 2004). Polar bears (*Ursus maritimus* Phipps) occasionally visit, drifting on ice to the shores of northern and northwestern Iceland from



**Fig. 1.6** The Arctic Fox, the only Icelandic land mammal that was living in Iceland before the settlement (Courtesy Daníel Bergmann)

Greenland, but such stragglers are usually killed soon after their arrival (Haraldsson and Hersteinsson 2004; Skírnisson 2009; Sæmundsson et al. 2009). Four species of rodents arrived with man; the Long-tailed Field Mouse (*Apodemus sylvaticus* L.), the House Mouse (*Mus musculus* L.), the Brown Rat (*Rattus norvegicus* Berkenhout), and the Black Rat (*Rattus rattus* L.). The Field Mouse is common throughout the country and the House Mouse and the Brown Rat are common in towns and villages; the Black Rat occurs sporadically in Reykjavík and other ports (Skírnisson 2004a, b, c, d).

Two further mammal species have been introduced by man in more recent times; the Reindeer (*Rangifer tarandus* L.), now living in the wild in eastern Iceland (Þórisson 2004), was introduced from Norway and Finland, and the Mink [*Mustela vison* Schreber, syn. *Neovison vison* (Schreber) Abramov], a North American musteline introduced for fur-farming that subsequently escaped from captivity and has steadily multiplied and spread over large areas (Skírnisson et al. 2004).

A distinctive feature of the fauna of Iceland is the complete absence of reptiles and amphibians.

In total, ca 349 species of birds have been reported from Iceland (Petersen 1998). Of these, 75 nest regularly, one species has become extinct worldwide (the Great Auk, *Pinguinus impennis* L.) and two species have become extinct on the island (the Water Rail, *Rallus aquaticus* L. and the Little Auk, *Alle alle* L.). Six species are winter visitors, seven species are regular migrants, and the remaining ca 259 species are drifters or accidental. Of the drifters, ca 40 species visit the island regularly every year (Petersen 1998). The best known Icelandic bird is the Icelandic Gyrfalcon (*Falco rusticolus* L.; Fig. 1.7). The huge White-tailed Eagle (*Haliaeetus*



**Fig. 1.7** The Icelandic Gyrfalcon seen from below during flight (Courtesy Ólafur Karl Nielsen)

*albicilla* L.) was fairly common in Iceland, but now comprises only a few nesting pairs and is listed as a threatened species (Petersen 1998).

Very few species of fish have been reported in the fresh water lakes and rivers on Iceland. The most common are the Salmon (*Salmo salar* L.), the Trout (*Salmo trutt*a L.) and several varieties of the Arctic Char (*Salvelinus alpinus* L.; Jónsson and Pálsson 2006).

More than 90 species of spiders and 800 species of insects have been recorded on Iceland. Among insects, the diptera (flies, gnats, and midges) represent the largest and most important group. Beetles, bees, and butterflies are also fairly well represented, but ants are entirely lacking (Guðmundsson 1975; Einarsson 1989). Fresh water bivalves and gastropods and land snails are quite common (Mandahl-Barth 1938).

The marine mammalian fauna in Icelandic waters is composed of ca 23 species of whales and dolphins, and about seven species of seals and walrus. Although most of the whales migrate to Iceland in springtime and leave in the autumn, others (ca nine species) are rarely seen (Hersteinsson 2004). Only two species of seals breed along the islands shorelines; the Common Seal (*Phoca vitulina* L.; Hauksson et al. 2004) and the Grey Seal (*Halichoerus grypus* Fabricius; Hauksson and Ólafsdóttir 2004). Occasionally, the Walrus (*Odobenus rosmarus* L.) visits Iceland as a single straggler or in pairs (Þórðarson and Hauksson 2004).

About 340 species of marine fish have been recorded from Icelandic waters (Jónsson and Pálsson 2006). Approximately one third of these are known to breed in the seas and shallows around Iceland. Others are regarded as rare migratory visitors or accidental stragglers from more oceanic waters; these are mostly

bathypelagic species of southern origin (Hallgrímsson 1975; Jónsson 1983; Jónsson and Pálsson 2006).

The marine invertebrate fauna is mainly composed of arctic-boreal and boreal species. Most have also been found in western European waters and some American species occur as well. In 1975, marine annelids belonging to the polychaete worms constituted about 225 species, amphipod crustaceans about 185 species, non-parasitic crustaceans about 170 species, bivalves about 95 species, gastropods about 130 species, and echinoderms about 90 species (Hallgrímsson 1975). Since then, these numbers have increased, mainly due to the BIOICE-project (Guðmundsson et al. 1999), during which several new species have been reported in Icelandic waters.

After the Pliocene closure of the Central American Seaway at ca 3.6 Ma, the flow of surface water from the Pacific through the Bering Strait and Arctic Ocean brought a tide of Pacific marine invertebrates to Iceland and the North Atlantic, including molluscs (gastropods and bivalves), brachiopods and echinoderms (Durham and MacNeil 1967; Backman 1979; Símonarson and Eiríksson 2008; see Chap. 10). This migration included several well-known species of common occurrence in the North Atlantic today, including the Blue Mussel (*Mytilus edulis* L.), Northern Horsemussel (*Modiolus modiolus* L.), Greenland Smooth Cockle (*Serripes groenlandicus* Mohr), *Ciliatocardium ciliatum* Fabricius, Arctic Hiatella (*Hiatella arctica* L.), Atlantic Great or Oval Paddock (*Zirfaea crispata* L.), Common Whelk (*Buccinum undatum* L.), and the Rejected Neptune (*Neptunea despecta* L.). Additionally, several Pacific species reached Iceland during the Pleistocene; amongst them is the well-known Blunt Gaper (*Mya truncata* L.).

## 1.5 Opening of the Northern North Atlantic and the Birth of Iceland

Geological evidence shows that the East Greenland continental margin (part of the North American Plate) began to move away from the Scandinavian and the British Isles margin (part of the Eurasian Plate) by rifting and sea-floor spreading close to anomaly 24, in the early Palaeogene (ca 55 Ma; Talwani and Eldholm 1977; Soper et al. 1976; Larsen 1978; Eldholm et al. 1994). When the plates first started to drift apart, the magma generated by a mantle plume hotspot in this area formed a connection or ‘land bridge’ between North America/Greenland and Europe (Nilsen 1978). This ridge, nowadays mostly submarine, is known as the Greenland-Scotland Transverse Ridge (GSTR). Iceland, which lies on the GSTR is the surface expression of the hotspot, which currently lies at the boundary of the North American and Eurasian plates (Vink 1984).

The continental break-up and related volcanism caused the formation of extensive basaltic lava successions in the northern North Atlantic area (Fig. 1.8), found in Eastern Greenland, Iceland, the Faeroe Islands, Scotland (Ardnamurchan, Skye, Rhum, Arran) and Northern Ireland (Giants Causeway; Dickin 1988; Pedersen et al. 1997; Saunders et al. 1997). In the early Cainozoic, the Eurasian and North

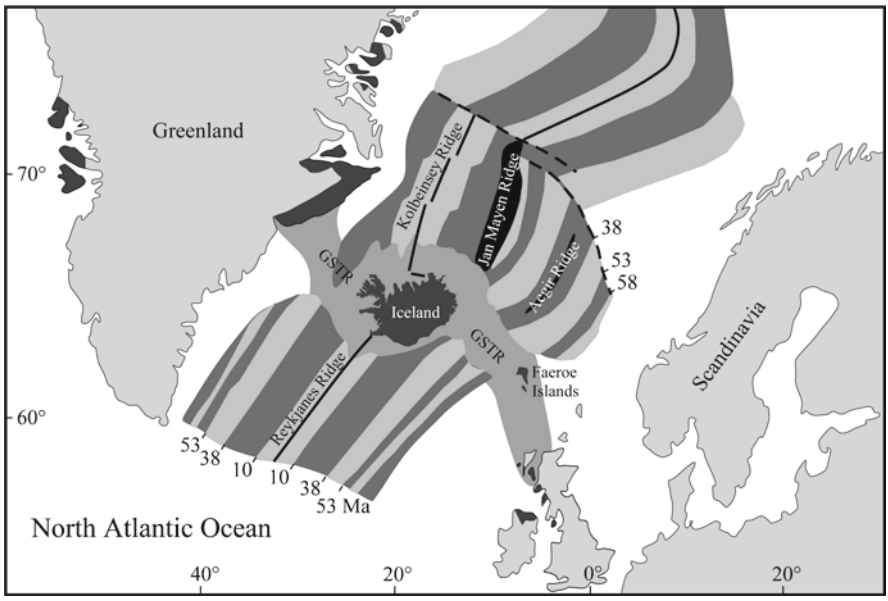



**Fig. 1.8** Schematic map showing the geographical position of Iceland, with the Mid-Atlantic Ridge crossing the island, the Reykjanes Ridge on the south-western side and the Kolbeinsey Ridge on the northern side. Terrestrial Cainozoic basalt successions in Greenland, Iceland, the Faeroe Islands, and the British Islands are indicated with *dark grey* colour. Anomalies of the ocean floor (*different shades of grey*) as well as relative age (numbers in Ma) are shown. The general outline of the Greenland-Scotland Transverse Ridge (*GSTR*) is indicated (Modified after Talwani and Eldholm 1977; Larsen 1980; Steinþórsson 1981)

American plates were close enough for the plume magma to sustain a complete subaerial connection (continuous land bridge) between Greenland and the European mainland. However, during the Neogene, as the northern North Atlantic Ocean widened and subsided, the marginal eastern and western parts of this transverse ridge cooled and were gradually submerged. When, how and to what extent this land bridge broke down is a matter of dispute (see Chap. 12), but it seems that parts of the transverse ridge (other than oldest parts of present-day Iceland) were still above sea level in the Middle Miocene (Nilsen 1978; Thiede and Eldholm 1983; Eldholm et al. 1994; Poore 2008).

## 1.6 Tectonic and Mantle Plume History of Proto-Iceland

After the initial spreading, the East Greenland and the European continental margins became submarine (Fig. 1.9), but the mantle plume kept the GSTR (including proto-Iceland and the Faeroe Islands) above sea level at 60–50 Ma. At this time, the mantle plume is thought to have been located under East Greenland, west of the Scoresby Sound (Vink 1984). Extrusive basalts in this region have been dated to

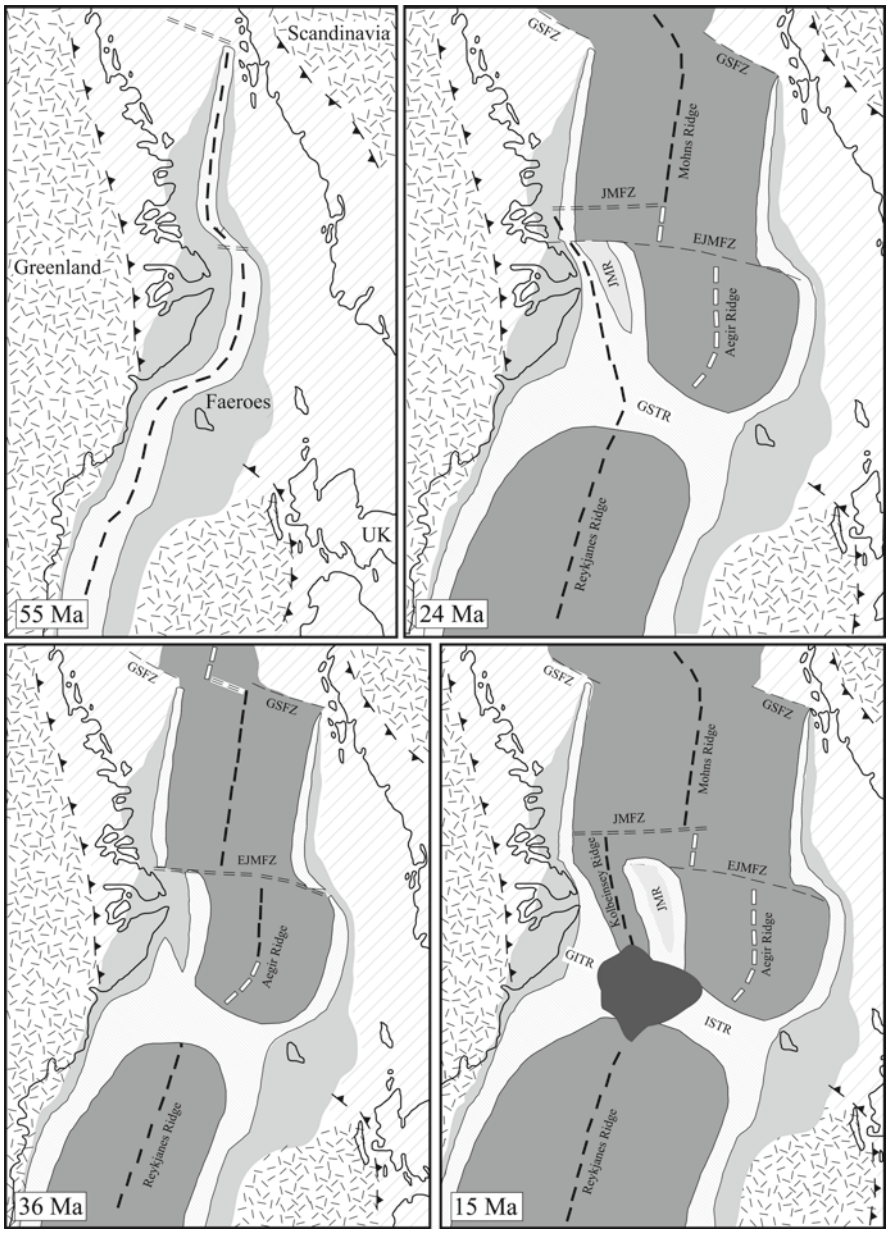



**Fig. 1.9** Schematic reconstruction showing the opening of the northern North Atlantic, widening of the ocean, rift history of the area, and the "birth" of Iceland. *GSFZ* Greenland Senja Fracture Zone, *EJMFZ* East Jan Mayen Fracture Zone, *JMFZ* Jan Mayen Fracture Zone, *JMR* Jan Mayen Ridge, *GSTR* Greenland-Scotland Transverse Ridge (Modified after Larsen 1978, 1980; Vink 1984)

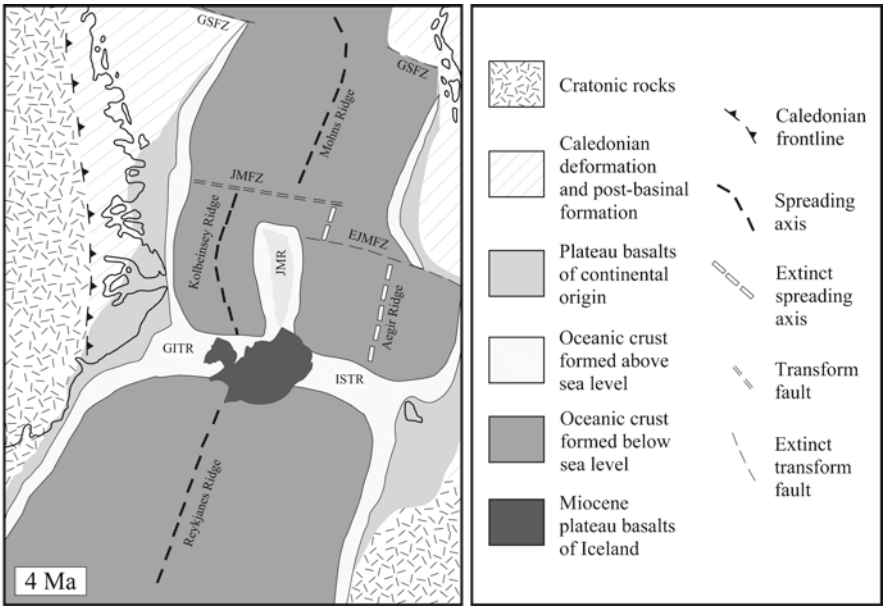



**Fig. 1.9** (continued)

60–55 Ma (Beckinsale et al. 1970). Later, the mantle plume moved (in relative terms) from underneath the Greenland continental shelf and at 36 Ma it lay under oceanic crust, feeding the then active Reykjanes Ridge, south of proto-Iceland, and the Aegir Ridge to the north. The oldest volcanic successions east and west of Iceland, formed at 55–36 Ma (anomalies 25–16), originated from these ridges (Fig. 1.9). When the spreading activity along the Aegir Ridge, north of proto-Iceland, ceased at 27 Ma the Kolbeinsey Ridge took over (Vogt et al. 1980; Larsen 1980). Apparently the spreading centre of the now inactive Aegir Ridge jumped westwards closer to the mantle plume, activating the Kolbeinsey Ridge. Activity along the Kolbeinsey Ridge led to the separation of part of the East Greenland continental margin (Fig. 1.9), now known as the Jan Mayen Ridge (Talwani and Udintsev 1976; Talwani and Eldholm 1977). At around 20 Ma, all seafloor spreading north of Iceland took place along the Kolbeinsey Ridge (Vink 1984).

## 1.7 Tectonic and Rift Relocation History of Iceland

Due to steady spreading along the Mid-Atlantic Ridge that separates the Eurasian and the American plates and therefore divides Iceland into two parts, the island widens approximately 20 km/Ma (Steinþórsson 1981) along the central inland rift zone (known as the Western Rift and the Northern Rift Zones). In a simplified

overview, the geological successions become younger towards the centre of the island. But, as the rift zones in Iceland continually become inactive and new rift zones are formed closer to the mantle plume, older successions are broken up, tilted, eroded, and separated by new younger geological constructions. The rift zones show repeated eastward relocation of the spreading axis in response to westward migration of the plate boundary relative to the plume centre, which seems to be quite stable (Steinþórsson 1981). At 24–15 Ma, the main spreading activity on land was located in the Northwest Iceland Rift Zone, now submarine off the northwest coast, and around 15 Ma a new rift zone, the Snæfellsnes-Húnaflói Rift Zone (see anticline axis on the Snæfellsnes peninsula in Fig. 1.10), evolved to the east (Harðarson et al. 1997, 2008). At 7–6 Ma, the southern part of the Snæfellsnes-Húnaflói Rift Zone became extinct and the presently active Western Rift Zone developed (Fig. 1.10). Then, at about 3–2 Ma the northern part of the Snæfellsnes-Húnaflói Rift Zone also became extinct and the presently active Northern Rift Zone formed (Jóhannesson 1980). This continuous rift relocation has had an important effect on the geology of Iceland, and, among others, caused massive erosion and deposition, forming extensive sedimentary formations that often contain plant and, in some rare cases, animal fossils.

## 1.8 Geological Outline of Iceland

Geologically, Iceland is a young volcanic island, built up during the later part of the Cainozoic. It is located on top of a mantle plume and at the junction of two submarine ridges, the Mid-Atlantic Ridge (active spreading boundary) and the GSTR (topographic relief caused by the presence of the Icelandic mantle plume at the plate boundaries). The mid-oceanic ridge bordering Iceland is represented by two segments, the Reykjanes Ridge in the south and the Kolbeinsey Ridge in the north (Fig. 1.8). These ridges are the submarine segments of the Mid-Atlantic Ridge that are closest to Iceland. The inland part of the mid-ocean ridge is characterized by rift zones or volcanic zones with active faulting and volcanism extending from the southwest to the north (Fig. 1.10). Spreading and volcanism takes place on discrete fissure swarms, 10–100 km long, known as volcanic systems. These systems are characterized by extensional tectonic features, open fissures, tensional cracks, graben structures, dikes, normal faults, and volcanic fissures, crater rows, small or large craters, cinder or spatter cones, and shield volcanoes. The most active part is generally in the middle and is often the site of a central volcano, such as a caldera or a stratovolcano (Saemundsson 1979; Steinthórsson and Thorarinsson 1997).

The rocks in Iceland are predominantly volcanic and are divided into four stratigraphic units or groups, the boundaries of which are defined by changing rock types (sedimentary and/or volcanic) and/or by their palaeomagnetism (Fig. 1.10). These four groups are: the Miocene-Pliocene Succession 16–3.1 Ma; the Pliocene-Pleistocene Succession 3.1–0.78 Ma; the Upper Pleistocene Succession 0.78 Ma to 11.5 ka; and the Holocene Succession 11.5 ka to Recent (Saemundsson 1979; Steinthórsson and Thorarinsson 1997).

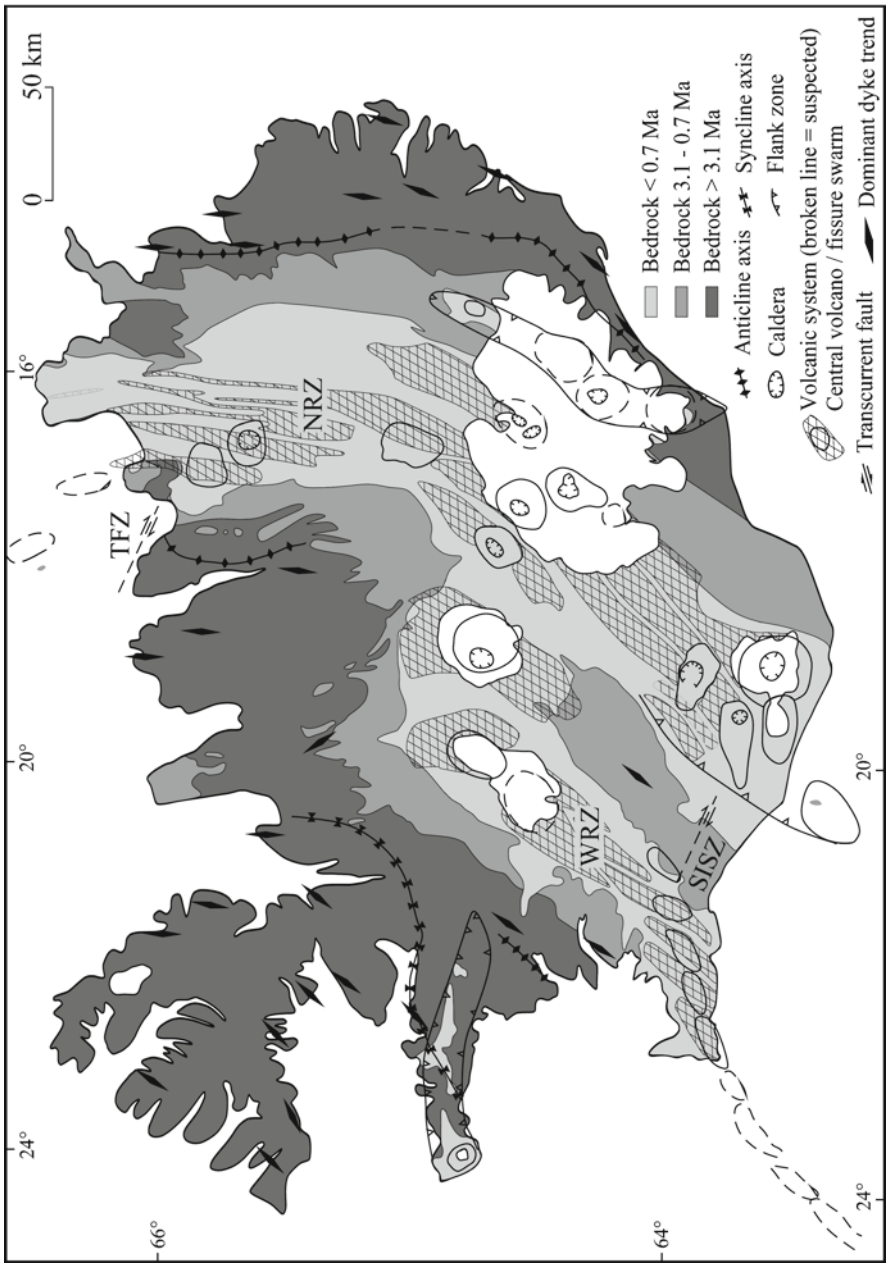



**Fig. 1.10** Geological map of Iceland showing the basic bedrock geology, the presently active rift and volcanic zones, anticline axis, syncline axis, transcurrent faults, and volcanic systems. *WRZ* Western Rift Zone, *NRZ* Northern Rift Zone, *TFZ* Tjörnes Fracture Zone, *SISZ* South Iceland Seismic Zone (Modified after Saemundsson 1974; 1979; Jóhannesson 1980; Jóhannesson and Sæmundsson 1989)

The Miocene-Pliocene Succession, 16–3.1 Ma (Fig. 1.10), comprises the oldest geological units on Iceland, built up during the Middle to Late Miocene and Pliocene. The succession covers an area of over 50,000 km$^2$ and includes the plateau basalt series typical of northwestern, western, northern, and eastern Iceland (Fig. 1.11).

This succession is mostly composed of tholeiitic lava flows and generally associated intermediate and acidic rocks. Volcanic activity during the Miocene and Pliocene was similar as today, confined to volcanic systems mainly along eruptive fissures and shield volcanoes (basaltic) or central volcanoes (calderas, stratovolcanoes; basaltic, intermediate and acidic). The most common intrusions are basaltic dikes which run vertically through the lava series. The majority of the dikes are oriented northeast-southwest as the central rift zone (Western Rift Zone-Northern Rift Zone). Central volcanoes were fed by magma from chambers underneath the volcanoes and when activity ceased the magma in the chamber solidified as plutonic rocks of gabbro or granophyre. Many plutonic intrusions in the Miocene-Pliocene Succession originated in this way (Saemundsson 1979; Steinthórsson and Thorarinsson 1997). The succession includes all the oldest and more than half of all the fossiliferous sedimentary rock formations discussed in this book (see Chaps. 4–10).

The younger Pliocene-Pleistocene Succession, from 3.1 to 0.78 Ma (Fig. 1.10), covers about 25,000 km$^2$ of land and occupies mostly the area between the older Miocene-Pliocene Succession and the younger Upper Pleistocene Succession. Volcanic rocks from the Upper Pliocene and Pleistocene in Iceland differ from the Miocene-Pliocene rocks, depending on whether they were erupted during intergla-



**Fig. 1.11** Typical basaltic lava flow series from Mount Skor and Stálfjall on the Northwest Peninsula, northwestern Iceland (Courtesy Oddur Sigurðsson)

cials or subglacially during glacial periods. During interglacial times, the volcanic activity was similar to that in the Middle to Late Miocene and Early to Middle Pliocene, but during glacial periods of the Late Pliocene and Pleistocene magma erupted underneath ice sheets of different thicknesses. Then the volcanic products accumulated in meltwater supported by the ice walls. Initially, pillow lavas formed but later on explosive activity started and the magma was quickly cooled by water and disintegrated into tephra. The basaltic glass in the tephra was altered to brown



**Fig. 1.12** Hyaloclastite ridges originating from volcanic fissure eruptions below thick icecaps. Skaftá, southern Iceland (Courtesy Oddur Sigurðsson)

palagonite which was cemented together as hyaloclastite (móberg). Hyaloclastite mountains (Fig. 1.12) mainly grew on fissures and formed ridges underneath the large icecaps. If the magma reached the surface of the ice, table mountains were formed when the hyaloclastites were capped by a lava shield and the melt water from the ice could no longer reach the erupting magma (Saemundsson 1979; Steinthórsson and Thorarinsson 1997). Sediments are sometimes much thicker in the Pliocene-Pleistocene successions than in the older Miocene-Pliocene succession, since fluvial, glacial, and marine related erosion as well as sedimentation due to isostatic changes were much more frequent. Plant bearing sediments were mainly accumulated during interglacial periods (see Chap. 11).

The Upper Pleistocene Succession, 0.78 Ma to 11.5 ka, covers about 30,000 km$^2$ of land and is essentially identical with the now active volcanic zones (Fig. 1.10). The strata of this succession were formed during the Brunhes palaeomagnetic chron (0.78 Ma to 11.5 ka; corresponding to Middle and Upper Pleistocene), continuing up to the Holocene. The volcanic rocks of this period are mostly interglacial basaltic lavas and subglacial pillow lavas and hyaloclastites (Saemundsson 1979; Steinthórsson and Thorarinsson 1997). The youngest flora investigated for this book (Svínafellsfjall Formation, see Chap. 11) is derived from the boundary between the Pliocene-Pleistocene and Upper Pleistocene successions.

The Holocene Succession, 11.5 ka until Recent, is composed of recent lava flows and pyroclastics, marine sediments, glacial sediments and soil formed after the retreat of the icecaps. Holocene volcanism has been confined to the now active volcanic/rift zones. Plant remains from this succession are not dealt with in this book.

## 1.9 Fossiliferous Sedimentary Rocks

Miocene to Holocene sediments in Iceland are mostly of volcanic origin, ranging from thin ash layers (very fine tuff; Fig. 1.13) to thick pyroclastic formations and ignimbrites. The grain size ranges from finest ash and lapilli tephra to large blocks and bombs (fine tuff, lapilli tuff, and volcanic breccias). The thickness of the sedimentary units can easily change over short distances, and the difference in grain size from one outcrop to the other is often substantial. All the Miocene, Pliocene, and Pleistocene ash layers, tephra, scoria beds, plinian pumice deposits, various pyroclastic units, and phreatoplinian deposits, as well as clastic- and organic sediments have been subjected to burial diagenesis and low-grade metamorphism (to Zeolite facies) due to loading and burial (Walker 1960; Roaldset 1983). Additionally, the uppermost parts of sedimentary units have often been subjected to thermal metamorphism by overlying lava (Roaldset 1983). Because of this, no loose sediments are found from the Miocene, Pliocene, and Pleistocene; all particles have been compacted, cemented and lithified, forming hard and often glassy sedimentary rock. Loose sediments are only known from the Holocene of Iceland.



**Fig. 1.13** Fine blackish and whitish ash layers in a Holocene soil section (Photo taken by Sigurður Þórarinsson)

Clastic sedimentary rocks from the Miocene to Pleistocene are also quite variable with different types of clays, siltstones, sandstones, and conglomerates, as well as tillites. These rocks reflect a diverse origin, having accumulated in lagoons, lakes, river channels, and alluvial fans, in deltas, on flood plains, in marshlands and swamps, around glaciers, or in other landforms (Thorarinsson 1963; Grímsson 2002, 2007a, b; Grímsson et al. 2007). Relatively thin palaeosoils and aeolian silt- and sandstones of reddish colour are also prominent in the Miocene and Pliocene strata; they frequently separate lava flows (Fig. 1.14). Lacustrine sedimentary rocks from the Miocene to Pleistocene are often present and usually have a rather limited distribution, except when formed in connection with rift relocation, but may be of considerable thickness. The lacustrine rocks typically consist of thin-bedded shales, mudstones and siltstones interfingered with turbidites and overlain by coarser deltaic deposits of sandstone and conglomerate (Grímsson 2007a, b). In the Pleistocene, drop-stones become prominent in glacial related environments. Fluvial sediments from the Miocene to Pleistocene, reflecting river channels and flood plains, occur as large lenses of sandstone and conglomerate with surrounding thin-bedded shales that reappear and interfinger with coarser sedimentary rocks. Delta marshlands and swamp deposits from the Miocene to Pleistocene are often found as various types of fine- to coarse-grained, organic rich and dark coloured sedimentary rock (Grímsson 2007a, b). These units are rich in plant remains (detritus) and are accompanied by numerous lignites or coal



**Fig. 1.14** Red coloured sedimentary rocks between basaltic lava flows at Þuríðará river in Vopnafjörður, eastern Iceland

beds (Fig. 1.15), especially in the Miocene-Pliocene Succession. Other types of organic sedimentary rocks are not as common except for yellow to whitish diatomite that accumulated in freshwater environments (Friedrich 1968; Grímsson 2007a, b), and have been found mostly in Miocene strata.

Depending on the sediment origin, accumulation rate, type of sediment and different taphonomic processes, the sedimentary rocks contain no or abundant plant fossils. To date, numerous plant fossils of angiosperms, gymnosperms, mosses, club mosses, ferns, and horsetails have been recorded. Plant parts that have been recovered include roots, rhizomes, stems, branches, shoots, leaves, fronds, isolated pinnae, cuticles, catkins, seeds, fruits (capsules, cones, and samaras), cone scales, pollen, and spores.

The oldest Miocene plant fossils are approximately 15 Ma old and are found in sedimentary rocks in northwestern Iceland (Table 1.2; see Chap. 4, Fig. 4.1). Slightly younger fossiliferous sedimentary rocks, 12–8 Ma old, are also found on the Northwest Peninsula (Table 1.2; see Chaps. 5–7, Fig. 5.1, Fig. 6.1, Fig. 7.1). Fossils from the latest Miocene are found around Lake Hreðavatn in western Iceland (Table 1.2; see Chap. 8, Fig. 8.1) and in Fnjóskadalur in the north (Table 1.2; see Chap. 9, Fig. 9.1). Plant remains from the Pliocene and Pleistocene are known

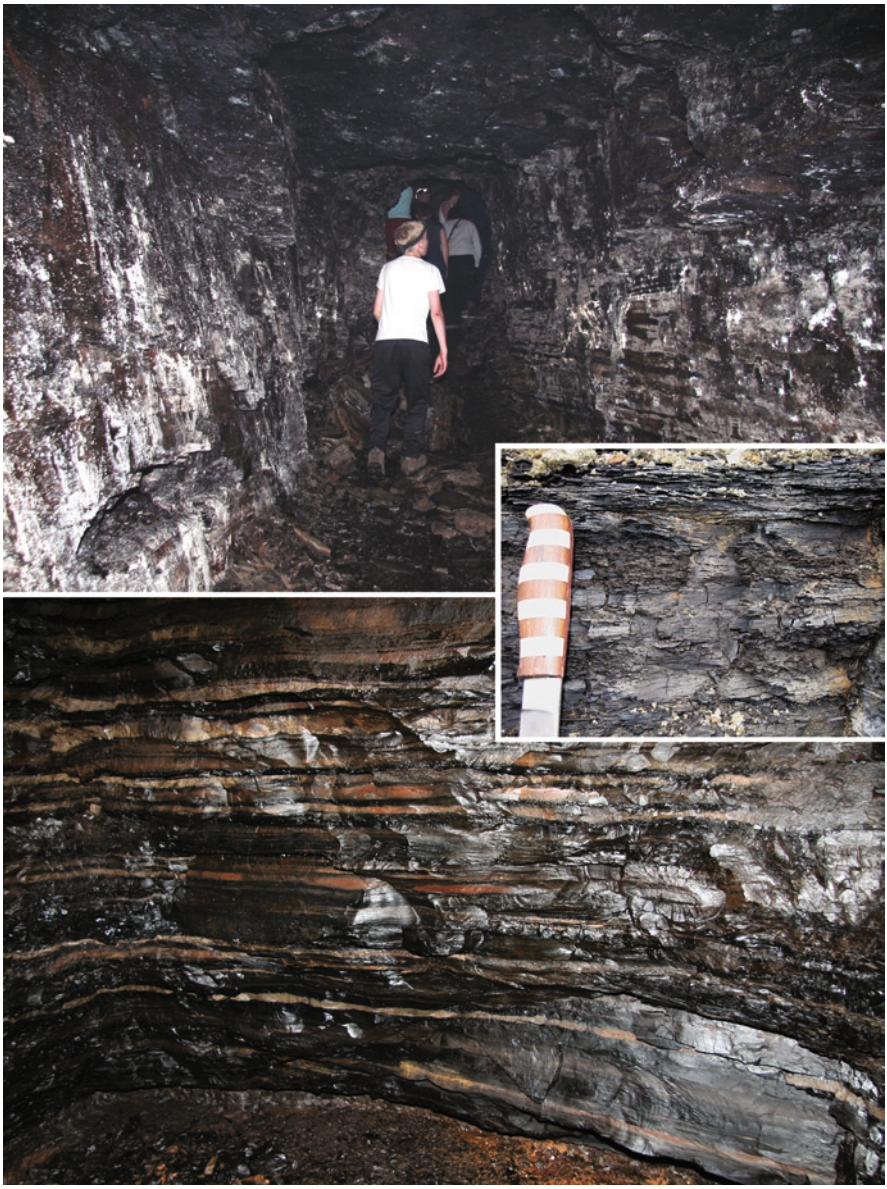


**Fig. 1.15** Lignite mine in Mount Stálfjall at Stálvík, northwestern Iceland. Upper photo showing entrance to the mine, and the lower one a close up of the mined lignite surface (Courtesy Ólafur Sigurðsson). Small photo showing typical weathered lignite from the Húsavíkurkleif outcrop in Steingrímsfjörður, northwestern Iceland

**Table 1.2** Chronology of Miocene to Pleistocene fossiliferous sedimentary formations and biozones mentioned in the following chapters

| Age | Formation/beds/biozone | Plant fossil localities | Discussion |
|---|---|---|---|
| 0.8 Ma | Svínafellsfjall Formation | Svínafell | Chapter 11 |
| 1.1 Ma | Búlandshöfði Formation | Stöð | Chapter 11 |
| 1.7 Ma | Víðidalur Formation | Bakkabrúnir | Chapter 11 |
| 2.4–2.1 Ma | Brekkukambur Formation | Miðsandsdalur, Gljúfurdalur, Litlasandsdalur | Chapter 11 |
| 4.4–3.8 Ma | Tjörnes beds (Tapes and Mactra zones) | Egilsgjóta, Reká, Skeifá | Chapter 10 |
| 5.5 Ma | Fnjóskadalur Formation | Selárgil | Chapter 9 |
| 7–6 Ma | Hreðavatn-Stafholt Formation | Stafholt, Laxfoss, Veiðilækur, Brekkuá, Snóksdalur, Hestabrekkur, Giljatunga, Fífudalur, Þrimilsdalur, Fanná, Langavatnsdalur | Chapter 8 |
| 9–8 Ma | Skarðsströnd-Mókollsdalur Formation | Tindafjall, Hrútagil, Broddanes | Chapter 7 |
| 10 Ma | Tröllatunga-Gautshamar Formation | Margrétarfell, Gautshamar, Belti, Torffell, Stekkjargil, Winklerfoss, Gunnustaðagróf, Nónöxl, Bæjarfell, Húsavíkurkleif, Hleypilækur, Fætlingagil, Grýlufoss, Dettifoss, Merkjagil, Hjálparholt, Bæjarlækur, Nónlækur | Chapter 6 |
| 12 Ma | Brjánslækur-Seljá Formation | Seljá, Surtarbrandsgil | Chapter 5 |
| 15 Ma | Selárdalur-Botn Formation | Þórishlíðarfjall (Selárdalur), Botn | Chapter 4 |

from the Tjörnes peninsula, northern Iceland (Table 1.2; see Chap. 10, Fig. 10.1), the Snæfellsnes peninsula and Víðidalur in western Iceland, and Svínafell in Öræfi in southern Iceland (Table 1.2; see Chap. 11, Figs. 11.1, 11.2, 11.4–11.6).

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# Chapter 2
# A Brief Review of Palaeobotanical Research in Iceland

**Abstract** The development of palaeobotanical research in Iceland reflects the emergence of palaeobotany as a science in Central Europe and has traditionally been closely tied to research activities in Denmark and Sweden. A major impetus for palaeontological research in Iceland and other Arctic areas came from the Swiss palaeontologist Oswald Heer, commencing in the mid-nineteenth century. Modern palaeontological research reflects current trends in palaeontology, namely, reconstructing climate changes and evolution from fossil plants and animals, and evaluating the importance of Iceland as part of a land bridge for intercontinental plant migration across the northern North Atlantic. Today, palaeontology has become closely tied to biology and a synthetic approach is emerging inferring biogeographic histories from phylogenies derived from modern organisms and from fossils.

## 2.1 Introduction

Organised palaeontological investigations in Iceland started in the early nineteenth century, although impressions of plants in sedimentary rocks had been known to local people long before that (cf. Friedrich and Símonarson 1981, 1983). The period of early geological and palaeontological investigations in Iceland coincided with both Denmark's interests in exploring the availability of fossil fuels and minerals on the island (Iceland was a Danish dependency until 1944) and the time of the first great scientific expeditions to explore the Arctic (e.g. Otto Torell's expedition to Iceland in 1857, Adolf Erik Nordenskiöld's Greenland expedition in 1883; cf. Liljequist 1993). At the same time, the first geological surveys were established in Europe; one of them the Geological Survey in Vienna, founded in 1849 by Wilhelm Ritter v. Haidinger (1795–1871). During this time, geological surveys began to link basic research, application-oriented geology and industry and motivated some of the German geological-palaeontological expeditions to Iceland (for example Schmidt and Keilhack's expedition of 1883, see below).

However, during the so-called 'pre-scientific period' (Mai 1995), Eggert Ólafsson (1772) had reported fossilised leaves of 'birch, rowan, and willow … and many most similar to oaks' from the Surtarbrandsgil locality, Northwest Iceland (see Chap. 5). Eggert Ólafsson (1726–1768), the son of a farmer of western Iceland, went to

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**Fig. 2.1** Icelandic farm (ca. 1760). Illustration from Ólafsson (1772), courtesy National Museum of Iceland. The picture should not be thought of as a landscape painting but as an unusually elegant schematic diagram (cf. Snorrason 1972; Ringler 1996–1998)

Copenhagen for his studies of natural sciences and grammar. When he returned to Iceland, he became a naturalist, writer, and important conservator of the Icelandic language (Hermannsson 1925). Together with Bjarni Pálsson, he made several trips to explore Iceland, between 1752 and 1757, to inventory the country's physical geography and mineral resources, on behalf of the Danish Royal Academy of Sciences. During these travels, they made the first recorded ascent of Mount Hekla (1,450 m a. s. l.), doing

so in the face of widespread popular belief that Hekla was one of the mouths of hell. These explorations resulted in by far the most detailed and comprehensive description of the natural conditions and inhabitants of Iceland at that time (Ólafsson 1772; Fig. 2.1).

## 2.2 The Emergence of Palaeobotany as a Branch of Science

In his lively written biography of Oswald Heer, Schröter (1887) summarised the initial development of palaeobotany as a branch of the sciences. During the eighteenth century, natural scientists had already commonly started to look upon fossils as documents of the past and in a paper communicated to the French Academy of Sciences in 1718, the botanist and physician Antoine de Jussieu (1686–1758) noted that ferns from the Carboniferous of France belonged to tropical groups of ferns and were not related to modern European ones (Jussieu 1718). From this, he concluded that the climate in Europe during the Carboniferous had been tropical. Most accounts on fossil plants from that time, however, were restricted to the description and illustration of eye-catching specimens, mainly from the Carboniferous, without attempting to relate them to modern analogues.

Both Mägdefrau (1956) and Mai (1995) regard Ernst Friedrich von Schlotheim (1765–1832) as the founder of modern palaeobotany. In a major work, Schlotheim (1820, 1822) was the first to describe fossil plants using the binomial nomenclature previously introduced by Carl von Linné (1753). In addition, Schlotheim recognised the value of plant fossils to determine the stratigraphic position/relative age of fossiliferous sediments and the climatic conditions under which they had been formed. At almost the same time, Kašpar Maria von Sternberg (1761–1838) in Prague and Adolphe Brongniart (1801–1867) in Paris, published important works on plants from earlier geological periods (Sternberg 1820–1838; Brongniart 1821; 1828; 1828–1837). These works, along with Schlotheim's, mark the beginning of palaeobotany, introducing, among other novelties, a stratigraphic framework comparable to what is now known as Palaeozoic, Mesozoic, and Cainozoic, and an attempt to use a natural system of classification for fossil plants. In his "*Flora der Vorwelt*", Sternberg (1820–1838) assumed three periods of vegetation, first, an insular period with great coal plants, second, a period with predominating cycadean types, and third, a period characterised by dicotyledonous plants.

When Charles Darwin (1809–1882) published "*On the Origin of Species*" in 1859, establishing modern ideas about evolution by common descent, the previous findings by palaeobotanists that more simple types of plants preceded more complex types received a theoretical basis and the importance of palaeontology as a science rapidly increased. This did not mean that palaeontologists immediately adopted Darwin's ideas. Examples are the changing view on Darwin's and Haeckel's ideas of Þorvaldur Thoroddsen (Erlingsson 2002) or the scepticism of Heer about Darwin's views (cf. Schröter 1887, pp. 350 ff.).

The works of Schlotheim, Sternberg and Brogniart and of Darwin, and even later of Alfred Wegener (1880–1930; Wegener 1915), provided the basis for modern palaeontology, historical biogeography, and phylogeny (see Sect. 2.4) although they were not always received with appreciation at the time of their first publication.

## 2.3 Palaeobotanical Investigations in Iceland

Scientific collecting of plant fossils in Iceland started in 1838 and 1839, when Japetus Steenstrup (1813–1897), a Danish zoologist, botanist and geologist collected plant fossils in the course of a geological survey of Iceland; he took the material back to Denmark, where it now is held at the Geological Museum in Copenhagen. Steenstrup worked for the Danish Finance Office (Rentukammer) and at first planned to explore natural resources in Iceland that might be exploited commercially, especially the sulphur in the region of Lake Mývatn in northern Iceland (Thoroddsen 1892–1904). In the summer of 1840, the famous Icelandic poet and naturalist Jónas Hallgrímsson (1807–1845) accompanied Steenstrup on extensive excursions over the island. During this exploration, they collected fossils in Surtarbrandsgil, in northwestern Iceland, and in the valley Langavatnsdalur and around lake Hreðavatn, in western Iceland. Steenstrup probably was the first person to explicitly state that the Tertiary flora of Iceland had a more North American character, whereas the modern flora was more European (Thoroddsen 1892–1904).

Gustav Georg Winkler (1820–1896), a Munich geologist and mineralogist visited Iceland in the summer of 1858 (Winkler 1861, 1863). He was sent to Iceland by King Maximilian II. of Bavaria, who was known as a monarch interested in arts and natural science, to investigate the geology of the island. Winkler collected fossils from Gautshamar, Húsavíkurkleif and Sandfell in northwestern Iceland. Winkler's and Steenstrup's collections of plant fossils, both stored at the Geological Museum in Copenhagen, formed the basis for Heer's description of the Miocene flora of Iceland in 1859 and 1868.



**Fig. 2.2** The Swiss naturalist Oswald Heer (1809–1883), photographed by O. Welti, Lausanne (from J. J. Heer 1885)

Oswald Heer (1809–1883; Fig. 2.2), the outstanding Swiss palaeontologist, was born in Niederutzwyl (modern spelling Niederuzwil) in the canton of St. Gallen. After studying theology and natural history in Halle, Germany, he became a pastor in Matt, canton Glarus, but soon started a career as a biologist. In 1835, he founded the botanical garden of Zurich and became its first director. In the following year, he became professor of botany and entomology at the University of Zurich. His first scientific contributions were on plant and insect distribution patterns in the Swiss Alps, and not until 1847 did he start to publish palaeontological work, starting with a pioneering work on Tertiary beetles in Europe (Heer 1847–1853). This was followed by his classic works on European and Arctic Tertiary plants "*Flora Tertiaria Helvetiae*" (three volumes, 1855–1859) and "*Flora fossilis arctica*" (seven volumes, 1868–1883). Heer was a keen mountaineer when young and he was the first to climb the Piz Linard, the highest peak in the Silvretta Group, Swiss Alps (3,413 m), on August 1, 1835 (Schröter 1889). However, his weak health soon made extensive collecting trips impossible and as a result he never visited Iceland. Consequently, he had to prepare his work on Miocene plants from Iceland (1859, 1868) on rather limited material, as some important plant fossil localities had not yet been discovered. Despite this, his approach was very modern in terms of both the taxonomic treatment and the way he estimated the Tertiary climate in the North Atlantic region (Heer 1859, 1868; see Chap. 13).

On its way to Greenland, Adolf Erik Nordenskiöld's (1832–1901) 1883 expedition made a stop in Iceland. Gustav Flink (1849–1932), then an undergraduate student, left the expedition at Eskifjörður in eastern Iceland and stayed on the island from June to early September, to conduct geological and mineralogical research. He collected several fossil plants at Tröllatunga in northwestern Iceland (see Chap. 6); these are now housed at the Swedish Museum of Natural History, Stockholm.

The first Icelandic naturalist to undertake extensive collecting of fossils in Iceland was Þorvaldur Thoroddsen (1855–1921; Fig. 2.3), born on Flatey, an island in Breiðafjörður, western Iceland. For his zoological, geological and geographic studies, he went to Copenhagen, Denmark, and Leipzig, Germany. Iceland still was



**Fig. 2.3** The Icelandic naturalist Þorvaldur Thoroddsen (1855–1921), photograph from Thoroddsen (1922–1923)

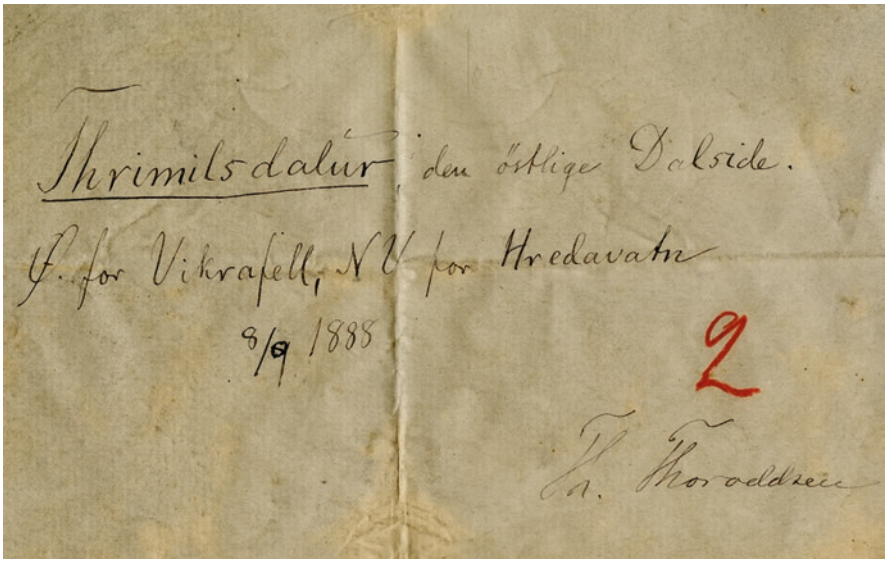



**Fig. 2.4** Original labels by Thoroddsen accompanying fossils donated to the Swedish Museum of Natural History

a Danish dependency and the University of Iceland was founded only in 1911. From 1881 to 1898 Thoroddsen undertook numerous expeditions in Iceland to explore the geography and geology of the island (Thoroddsen, 1892–1904; 1896; 1906; 1907–1922; 1913–1915). During this period, he had contacts with foreign geologists such as Flink, who collected for Nordenskiöld's 1883 expedition. A good deal of the plant fossils collected by Thoroddsen 1886 and 1888 went to the collections in Stockholm (Fig. 2.4) and formed part of the planned monograph by Nathorst (see Chap. 14).

Paul Windisch (1886a) prepared a doctoral thesis based on material collected from various localities in northwestern and eastern Iceland during the summer of 1883 by Carl W. Schmidt and Konrad Keilhack (1858–1944), from the 'Königliche Preussische Geologische Landesanstalt' in Berlin (Geological Survey). Schmidt studied rhyolites (Schmidt 1885), while Keilhack carried out research on geothermal activity, glacial phenomena, and general geology resulting in various publications (Keilhack 1883, 1885, 1886a, b, 1925). Keilhack became well-known, among others, for his terms Weichsel, Saale, and Elster referring to the main Pleistocene glacial cold phases in Northwestern Europe. Schmidt collected fossils from Surtarbrandsgil and Tröllatunga, northwestern Iceland. Unfortunately, Windisch (1886a, b) did not figure these fossils in his study. According to him, the fossils were stored in the botanical collections of Leipzig but no record of them has been found there.

Alfred Gabriel Nathorst (1850–1921) was a botanist and geologist who became renowned as the founder of the Department of Palaeobotany at the Swedish Museum of Natural History in Stockholm in 1884, for the foundation of the excellent collection of fossil plants in Stockholm, for his work on Mesozoic plants and as an Arctic



**Fig. 2.5** The Icelandic naturalist Guðmundur G. Bárðarson (1880–1933) (Courtesy J. Áskelsson's family)

explorer. His early interests were in Pleistocene migrations of Arctic plants and in 1871 he collected Pleistocene fossils in Denmark, together with Japetus Steenstrup, who had earlier collected fossils in Iceland. A year later, Nathorst travelled to Switzerland and was introduced to Oswald Heer, who took a fatherly interest in Nathorst's career. Nathorst's later expeditions to Bear Island, Greenland, Kong Karls Land, and Spitsbergen, and the numerous publications on Palaeozoic and Mesozoic plant fossils from these regions, made him one of the most respected coryphées of his time. Except for his studies of Pliocene fossils from Japan and a few Palaeogene plant fossils from Spitsbergen, the bulk of Nathorst's scientific work covers Palaeozoic and Mesozoic palaeontology. Nathorst had some correspondence with Icelandic geologists, among which Guðmundur G. Bárðarson (1880–1933; Fig. 2.5) is by far the most well-known (it is unclear whether Nathorst was also involved in the large donations to the Swedish Museum of Natural History by Thoroddsen). While mapping the occurrence of lignites in Iceland, Bárðarson collected plant fossils in Mókollsdalur, northwestern Iceland. He sent fossils to Nathorst, who identified them, noting among others two different species of *Fagus* (beech; Bárðarson 1918). This may have been the starting point for a regular correspondence between Bárðarson and Nathorst and later Halle (becoming Nathorst's successor in 1917), reflected in the various donations of plant fossils Bárðarson made to the Swedish Museum of Natural History in 1910, 1917, 1921, 1922, and 1924 (Fig. 2.6).

In the twentieth century, plant fossils were studied by Jóhannes Áskelsson (1902–1961, Fig. 2.7), a geologist and palaeontologist with a strong interest in plant fossils. He was the first Icelandic scientist to focus mainly on palaeobotanical research, with studies on both macrofossils and pollen (Áskelsson 1938a, b, 1946a, 1954, 1956). Áskelsson was also the first to describe fossils from the oldest plant bearing formation in Iceland, at the Selárdalur locality (Áskelsson 1946b, 1957) and facilitated fieldwork for the German palaeontologist and geologist Martin Schwarzbach in the 1950s. He also provided samples to the Norwegian palynologist Svein B. Manum (cf. Manum 1962).

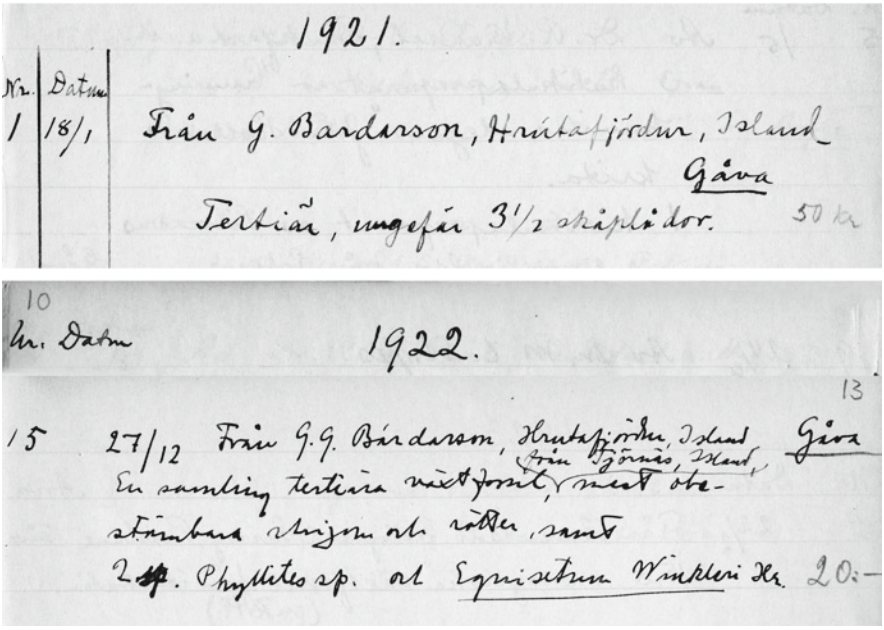



**Fig. 2.6** Two accessions (1921 and 1922; original note by Halle) of material collected by G. G. Bárðarson and donated to the Swedish Museum of Natural History, Stockholm

Martin Schwarzbach's (1907–2003) working group from Cologne focussed on fossil-bearing sedimentary rocks in Iceland, mainly during 1955 and 1970 (e.g. Schwarzbach 1955; Schwarzbach and Pflug 1957; Pflug 1959; Friedrich 1966). Hans-Dieter Pflug considered the sedimentary rocks of Iceland to be of Palaeogene age, based on the presence of pollen that he erroneously identified as Normapolles (Pflug 1956, 1959). This extinct pollen type resembles some modern members of Fagales and was particularly abundant during the Late Cretaceous and extending to the Early Oligocene (cf. the Normapolles Province, extending from western Siberia to Europe and eastern North America; Schönenberger et al. 2001; Friis et al. 2003). Pflug considered the pollen from Iceland to be similar to that found in Palaeogene sediments from Spitsbergen. Although Svein B. Manum (born 1926) did not suggest a particular age for the fossils of Iceland, he pointed out that the pollen grains Pflug had referred to Normapolles rather were of betulaceous affinity (Manum 1962). Later, Walter L. Friedrich (born 1938) studied macrofossils, pollen, and diatoms from the Brjánslækur-Seljá Formation (Friedrich 1966) and later published several accounts on the Icelandic Miocene floras and climate (Friedrich et al. 1972; Friedrich and Símonarson 1976, 1981, 1982, 1983).

During several visits in the 1970s, Mikael A. Akhmetiev (born 1935) and his co-workers (Akhmetiev et al. 1978) undertook a biostratigraphic correlation of Tertiary and Quaternary formations in Iceland, based mainly on palynological data.



**Fig. 2.7** Jóhannes Áskelsson (1902–1961), during a field trip with students (Courtesy Sigurður Steinþórsson)

They also collected macrofossils, now stored at the Icelandic Institute (Museum) of Natural History, in Reykjavík. This work provides an excellent overview of the many localities yielding plant fossils from both western and eastern Iceland. In addition, the first absolute age-datings and palaeomagnetic correlations for Icelandic basalts were published at that time (Kristjánsson 1968; Moorbath et al. 1968; Kristjánsson et al. 1975; McDougall et al. 1976a, b, 1977). This, for the first time, provided a robust stratigraphic framework, ruling out a Palaeogene age as assumed by previous palynological studies.

## 2.4 The Future: Palaeontology Meeting Phylogeny

During the past few decades, the study of northern hemisphere transcontinental disjunct distributions of plants experienced a renaissance that was linked to a new discipline in plant biogeography, phylogeography (Avise 2000). At first, molecular-based phylogenetic studies tried to reconstruct spatial patterns in the evolution of disjunctions, which then could be cross-checked against the tectonic history of the northern hemisphere. At the same time, it has become increasingly popular to estimate divergence times for closely related disjunct taxa (species, subgenera, etc.; cf. Donoghue and Benton 2007). For the northern hemisphere, the so-called North Atlantic Land Bridge (Tiffney 1985) provided excellent fossil evidence to complement molecular-based evidence for numerous Early Tertiary disjunctions in northern hemisphere angiosperms. However, due to the absence of clear terrestrial North Atlantic links between Eurasia and North America in the later parts of the Tertiary, this route has mainly been neglected for plant migrations during this period. Instead, the Bering Strait has been considered a vital bridge in the younger Tertiary (Tiffney and Manchester 2001).

In some cases, however, molecular studies indicate relatively young divergence times between clades that would imply a North American-European disjunction resulting from a broken link over the North Atlantic in relatively recent times. This led to a renewed interest in the North Atlantic as a possible corridor for plant migration during the Late Tertiary (Tiffney and Manchester 2001; Milne 2004, 2006) and emphasizes the paramount importance of Iceland as archive of Late Tertiary and Pleistocene plants in the North Atlantic. A recent evaluation of biogeographic affinities of fossils from Miocene sediments of Iceland strongly suggested that the North Atlantic Land Bridge continued to be suitable for intercontinental plant migration in the later parts of the Tertiary (Grímsson and Denk 2007). This can explain results from molecular studies approaching a similarly young divergence times for North American-western Eurasian disjunct plant taxa (Milne 2004; see also Chap. 12).

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# Chapter 3
# Systematic Palaeobotany

**Abstract** This chapter provides morphological descriptions including remarks on nomenclatural problems for the macrofossil (**M**) and palynological (**P**) record from Iceland. The systematic section starts with Bryophyta (mosses), Lycopodiophyta (clubmosses and spikemosses), and Pteridophyta (horsetails and true ferns), followed by Gnetophyta, Ginkgophyta, Pinophyta (conifers), and Magnoliophyta (flowering plants). Families and genera appear in alphabetical order. Incertae sedis are listed at the end of each large taxonomic group. For each taxon described, stratigraphic and geographic occurrences are provided. Remarks regarding systematic affinities to coeval and extant taxa are added as well. Most taxa described here are illustrated in the plates accompanying Chaps. 4–11. Macrofossils are stored in the Swedish Museum of Natural History (S), the Icelandic Institute (Museum) of Natural History (IMNH), and the Geological Museum, Copenhagen (GM). Pollen samples are kept at the Department of Palaeobotany, University of Vienna. A table summarizing all (morpho)taxa recorded from Iceland with their stratigraphic ranges is provided at the end of Chap. 12 (Appendix 12.1).

## 3.1 Bryophyta

### Amblystegiaceae

**aff. *Campylium* sp.** **M**

Moss pleurocarpous, slender, procumbent, sparsely and irregularly branched, preserved part of stem >2.1 cm long, 0.2–0.5 mm wide; several branches originating from stem, branches >3.0 cm long, 0.2–0.5 mm wide, leaves on stem and branches, equal in size, radially arranged but appearing alternately arranged in the compression fossil (two pairs per 2 mm stem, two to three pairs per 2 mm branches); leaves 1.4–2.2 mm long, 0.7–1.1 mm wide, erecto-patent (angle of divergence 10–23°), broadly ovate basal part, broadest in upper half of basal part, abruptly tapering to a narrow straight acumen constituting approx. 35–50% of leaf length; leaf margin clearly denticulate in upper to middle section of basal part, teeth small and sharp, acute; costa absent.

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*Occurrence*: 7–6 Ma sedimentary rock formation at Stafholt.

*Remarks*: The sedimentary context suggests this plant grew close to or in running water. This, together with the growth form of the plant indicates that it belongs to Amblystegiaceae, among which it shows closest affinity to *Campylium*.

### Sphagnaceae

#### *Sphagnum* sp. P

Plate 6.2, Figs. 7–12; Plate 9.2, Figs. 1–6; Plate 10.3, Figs. 1–3; Plate 11.2, Figs. 1–3; Plate 11.31, Figs. 1–3.

Spore, monad, shape oblate, outline triangular in polar view, equatorial diameter 14–26 μm under SEM, 12–35 μm under LM, trilete, laesurae 5–10 μm long (SEM), 6–12 μm long (LM), spore wall (exospore) 1.2–1.8 μm thick (LM), surface smooth, wall thickened around laesurae.

*Occurrence*: 10–0.8 Ma sedimentary rock formations at Tröllatunga (10 Ma), Selárgil (5.5 Ma), Tjörnes (Reká, 4.2–4.0 Ma), Bakkabrúnir (1.7 Ma) and Svínafell (0.8 Ma).

*Remarks*: Spores of different *Sphagnum* species may be morphologically very similar. However, based on the variability of the fossil material, especially size range and wall thickness in the distal polar area, more than one biological species could be involved in the Icelandic material.

#### Hepaticae gen. et spec. indet. P

Plate 5.2, Figs. 7–9.

Spore, monad, shape oblate, outline triangular in polar view, equatorial diameter 33–35 μm under SEM, 33–40 μm under LM, trilete, laesurae 12–20 μm long, extending to the equatorial flange, with curvaturae imperfectae, spore wall (exospore) 1.5 μm thick (LM), surface psilate (LM), granulate with sparsely spaced rugulae (SEM).

*Occurrence*: 12 Ma sedimentary rock formation at Surtarbrandsgil.

#### Brypohyta fam. et gen. indet. M

Plate 6.3, Figs. 1–2.

Moss acrocarpous, numerous unbranched leafy stems forming cushions; single stems from 4 mm to about 1.2 cm long; leaves spirally arranged, imbricate, 0.6–1 mm long, curving upwards, base broad, tapering in a long and slender apical part, midrib distinct.

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

## 3.2 Lycopodiophyta

### Lycopodiopsida

### Lycopodiaceae

***Lycopodiella* sp.** **P**

Plate 7.2, Figs. 1–6; Plate 10.3, Figs. 4–6.

Spore, monad, shape oblate, outline rounded-triangular in polar view, equatorial diameter 38–50 μm under SEM, and 40–63 μm under LM, trilete, laesurae 11–18 μm under SEM, 16–19 μm long under LM, laesurae three-fourths of the radius, with curvaturae imperfectae, spore wall (exospore) 2.2–3.3 μm thick (LM), sculpture on distal side rugulate, granulate, on proximal side slightly rugulate with verrucae along the laesurae (SEM).

*Occurrence*: 9–4.0 Ma sedimentary rock formations at Hrútagil (9–8 Ma) and Tjörnes (Reká, 4.2–4.0 Ma).

***Lycopodium* sp.** **P**

Plate 5.2, Figs. 10–15; Plate 6.3, Figs. 3–13; Plate 7.2, Figs. 7–12; Plate 9.2, Figs. 7–12; Plate 10.3, Figs. 7–9; Plate 11.2, Figs. 4–9; Plate 11.16, Figs. 1–3; Plate 11.31, Figs. 4–6.

Spore, monad, shape oblate, outline subtriangular in polar view, equatorial diameter 23–43 μm under SEM, and 25–50 μm under LM, trilete, laesurae 12–13 μm under SEM, 15–20 μm long under LM, exospore 3.1–4 μm thick (LM), sculpture on distal side heterobrochate reticulate, muri sometimes imperfect, more or less smooth in areas between muri, muri thin and high, sculpture on proximal side weak or lacking muri (SEM).

*Occurrence*: 12–0.8 Ma sedimentary rock formations at Surtarbrandsgil (12 Ma), Tröllatunga, Húsavíkurkleif (10 Ma), Hrútagil (9–8 Ma), Selárgil (5.5 Ma), Tjörnes (Egilsgjóta, Reká, Skeifá; 4.3–3.8 Ma), Bakkabrúnir (1.7 Ma), Stöð (1.1 Ma) and Svínafell (0.8 Ma).

*Remarks*: Based on the morphological variability observed in the material available, this morphotaxon might combine more than one natural species (up to four more or less distinct types). Variability within the taxon is mainly due to differences in the hight of muri, variations in reticulum and sculpture on the proximal side.

***Huperzia* sp.** **P**

Plate 6.2, Figs. 1–3; Plate 6.4, Figs. 1–9; Plate 7.3, Figs. 1–3; Plate 8.2, Figs. 8–10; Plate 10.3, Figs. 10–12; Plate 11.2, Figs. 10–12; Plate 11.16, Figs. 4–6.

Spore, monad, shape oblate, outline triangular in polar view with truncate apices, polar axis 22–26 μm, equatorial diameter 22–34 μm under SEM, equatorial diameter 24–41 μm under LM, trilete, laesurae 14–15 μm (SEM), 10–18 μm long (LM), distinctly ridged, with curvaturae imperfectae, spore wall 1.2–1.7 μm thick (LM), sculpture on distal side foveolate to fossulate, lumina usually rounded, broad muri, proximal surface smooth or weakly foveolate to fossulate (SEM).

*Occurrence*: 10–1.1 Ma sedimentary formations at Tröllatunga (10 Ma), Hrútagil (9–8 Ma), Hestabrekkur (7–6 Ma), Tjörnes (Reká, 4.2–4.0 Ma), Bakkabrúnir (1.7 Ma) and Stöð (1.1 Ma).

**Lycopodiaceae, gen. et spec. indet. 1** **P**

Spore, monad, shape oblate, outline triangular in polar view, equatorial diameter 31–50 μm under SEM, 40–66 μm under LM, trilete, laesurae 18–21 μm long, sculpture on proximal side reticulate, lumina rounded, 3.6–4.8 μm in diameter (SEM).

*Occurrence*: 4.2–4.0 Ma sedimentary rock formation at Tjörnes (Reká).

**Lycopodiaceae, gen. et spec. indet. 2** **P**

Plate 11.16, Figs. 7–9.

Spore, monad, shape oblate, outline rounded triangular in polar view, equatorial diameter 34–36 μm under SEM, 41–43 μm under LM, trilete, laesurae 11–12 μm long (SEM), 15–20 μm (LM), sculpture on distal side reticulate, perforate, muri crested, covered with microverrucae, proximal side microverrucate with few perforations (SEM).

*Occurrence*: 1.1 Ma sedimentary rock formation at Stöð.

**Isoetopsida**

**Selaginellaceae**

***Selaginella* sp.** **P**

Plate 10.4, Figs. 1–3.

Spore, monad, shape oblate, outline circular triangular in polar view, equatorial diameter 30–42 μm under SEM, 42–58 μm under LM, trilete, laesurae 15–19 μm long, spore wall 1.7 μm thick (LM), sculpture on proximal side granulate-perforate, echinate, echinae widely spaced, confined to distal side, echinae surface granulate (SEM).

*Occurrence*: 4.2–4.0 a sedimentary rock formation at Tjörnes (Reká).

## 3.3 Pteridophyta

### Equisetopsida

### Equisetaceae

***Equisetum* sp.** **M**

Plates 6.6, Figs. 8–9; Plate 8.2, Fig. 1; Plate 9.4, Figs. 1–4; Plate 10.2, Fig. 2

1859 *Equisetum winkleri* Heer – Heer: p. 317.
1868 *Equisetum winkleri* Heer – Heer: p. 140, pl. 24, figs. 2–6.
1975 *Equisetum* – Sigurðsson: fig. 10.
1886 *Equisetum* sp. (*Equisetum parlatorii* Schimper ?) – Windisch: p. 26.
1966 *Equisetum* sp. (cf. *Equisetum parlatorii* Heer; Schimper) – Friedrich: p. 57, pl. 1, fig. 8.
1978 *Equisetum* sp. – Akhmetiev et al.: pp. 178, 181, pl. 7, figs. 4, 7, pl. 12, figs. 10, 18, pl. 15, fig. 23.
2005 *Equisetum* sp. – Denk et al.: p. 371, figs. 2–4.

Fragments of aerial stems with nodes and leaves in whorls, leaves fused into a sheath, up to 11 leaves per axis width; underground rhizomes, nodules.

*Occurrence*: 12–1.7 Ma sedimentary rock formations at Seljá, Surtarbrandsgil (12 Ma), Tröllatunga, Gautshamar, Húsavíkurkleif (10 Ma), Hestabrekka, Brekkuá, Stafholt, Sandfell, Vindfell (7–6 Ma), Selárgil (5.5 Ma), Tjörnes (Reká, Skeifá; 4.2–3.8 Ma), Bakkabrúnir (1.7 Ma) and Svínafell (0.8 Ma).

*Remarks*: The number of leaves forming the sheath corresponds to that reported by Heer (1868) for *E. winkleri*. The remains of this type in the fossil record of Iceland are always fragmentary and it is possible that they reflect more than a single natural species. Further comparison to fossil and/or extant species is not meaningful.

### Polypodiopsida

### Osmundaceae

***Osmunda parschlugiana* (Unger) Andreánszky** **M**

Plate 5.2, Fig. 19; Plate 6.6, Figs. 1–5.

1978 *Osmunda heeri* Gaud. – Akhmetiev et al.: pp.178, 180, pl. 6, figs. 1, 2, 8, 9, pl. 11, fig. 5.
2005 *Osmunda parschlugiana* (Unger) Andreánszky – Denk et al.: p. 373, figs. 5–9.

Several fragmentary leaf apices and isolated pinnae; pinnae arranged alternately, up to 7.0 cm long and 2.0 cm wide, base asymmetrical, slightly cordate, apex blunt, margin finely crenulate, lateral veins rather dense, usually branching twice; all veinlets ending in sinuses.

*Occurrence*: 12–10 Ma sedimentary rock formations at Surtarbrandsgil (12 Ma) and Tröllatunga, Húsavíkurkleif, Margrétarfell and Hólmatindur (10 Ma).

*Remarks*: This genus was common in the Arctic Cainozoic and its records were published under different species names (see Boulter and Kvaček 1989). All belong to the *Osmunda regalis* L.-type. From Iceland, previous records of *Osmunda* were assigned to *O. heeri* (Akhmetiev et al. 1978). However, European foliage of the same morphology has usually been assigned to *O. parschlugiana* (Kovar-Eder et al. 2004), which is typified by a pinna from Parschlug (Early-Middle Miocene of Styria).

### *Osmunda* sp. (*Osmunda regalis* type) P

Plate 6.4, Figs. 10–12; Plate 6.5, Figs. 1–10; Plate 7.3, Figs. 4–9; Plate 10.4, Figs. 4–6; Plate 11.3, Figs. 1–3; Plate 11.16, Figs. 10–12.

Spore, monad, shape spheroidal to oblate, outline circular in polar view, equatorial diameter 25–50 μm under SEM, and 30–63 μm under LM, trilete, laesurae 10–21 μm under SEM, 15–22 μm long under LM, sculpture tuberculate to echinate, tubercles fused or solitary.

*Occurrence*: 10–1.1 Ma sedimentary rock formations at Húsavíkurkleif (10 Ma), Hrútagil (9–8 Ma), Tjörnes (Egilsgjóta, Reká, Skeifá; 4.3–3.8 Ma), Bakkabrúnir (1.7 Ma) and Stöð (1.1 Ma).

## Polypodiaceae

### *Thelypteris limbosperma* (All.) H. P. Fuchs M

Plate 11.32, Figs. 3–4.

Pinna, preserved parts up to 3.5 mm long, 1.3–2.0 cm wide, deeply lobed, pinnulae diverging from pinna axis at wide angles, pinnulae with a single central vein, from which four to ten pairs of lateral veins run towards the margin and sparsely branch close to margin; margin entire, slightly revolute, pinnulae 1.2–10 mm long, 1–3.5 mm wide, widest at base, apex bluntly acute, pinnulae longest in middle part of pinna, at least 11 pairs of pinnulae per pinna.

*Occurrence*: 0.8 Ma sedimentary rock formation at Svínafell.

### *Polypodium* sp. P

Plate 4.2, Figs. 1–3; Plate 6.7, Figs. 1–3; Plate 10.4, Figs. 7–9.

Spore, monad, shape oblate, outline elliptic in equatorial view, equatorial diameter 46–61 μm under SEM, 53–76 μm under LM, monolete, laesurae 18–24 μm long

(SEM), spore wall 3–3.5 μm thick (LM), spore surface verrucate; verrucae smooth, smaller close to laesurae (SEM).

*Occurrence*: 15–4.0 Ma sedimentary rock formations at Botn (15 Ma), Húsavíkurkleif (10 Ma) and Tjörnes (Reká, 4.2–4.0 Ma).

*Remarks:* High morphological variability observed in spores ascribed to *Polypodium* may indicate that they belong to more than a single natural species (possibly two spp.).

**Polypodiaceae gen. et spec. indet. 1** **P**

Plate 4.2, Figs. 4–6; Plate 5.2, Figs. 16–18; Plate 6.7, Figs. 3–5; Plate 7.3, Figs. 10–12; Plate 8.2; Figs. 5–7; Plate 9.3, Figs. 1–3; Plate 10.4, Figs. 10–12; Plate 11.3, Figs. 4–6; Plate 11.17, Figs. 1–3; Plate 11.31, Figs. 7–9.

Spore, monad, shape oblate, outline broadly elliptic in polar view, elliptic in equatorial view; polar axis 17–43 μm, equatorial diameter 28–45 μm under SEM, 20–43 μm and 33–51 μm under LM, monolete, laesurae 14–19 μm long under SEM, 17–26 μm under LM, spore wall 0.6–1.3 μm thick (LM), surface more or less psilate (SEM).

*Occurrence*: 15–0.8 Ma sedimentary rock formations at Botn (15 Ma), Surtarbrandsgil (12 Ma), Tröllatunga, Húsavíkurkleif (10 Ma), Hrútagil (9–8 Ma), Hestabrekkur (7–6 Ma), Selárgil (5.5 Ma), Tjörnes (Reká, Skeifá; 4.2–3.8 Ma), Bakkabrúnir (1.7 Ma), Stöð (1.1 Ma) and Svínafell (0.8 Ma).

*Remarks*: It is unclear whether these spores belong to a single natural species. Although the surface of all spores observed is smooth, many Polypodiaceae spores have a characteristic and diagnostic perispore, which is usually lost during fossilization and/or during preparation of the sediment.

**Polypodiaceae, gen. et spec. indet. 2** **P**

Plate 5.2, Figs. 4–6; Plate 10.5, Figs. 1–3.

Spore, monad, shape oblate, outline elliptic in equatorial view, polar axis 24–26 μm, equatorial diameter 34–35 μm under SEM, 30–32 μm and 44–45 μm under LM, monolete, laesurae 13 μm long (SEM), 23 μm (LM), spore wall (exospore) 0.7–1 μm thick (LM), sculpture rugulate, fossulate (LM, SEM).

*Occurrence*: 12–4.0 Ma sedimentary rock formations at Surtarbrandsgil (12 Ma) and Tjörnes (Reká, 4.2–4.0 Ma).

**Polypodiaceae gen. et spec. indet. 3** **P**

Plate 6.7, Figs. 6–8.

Spore, monad, shape oblate, outline elliptic in equatorial view, polar axis 25 μm, equatorial diameter 45 μm under SEM, 30 μm and 51 μm under LM, monolete,

laesurae 26 µm long, spore wall 0.7–1.3 µm thick (LM), sculpture on distal side rugulate, proximal side psilate, perforate (SEM).

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

**Polypodiaceae gen. et spec. indet. 4** **P**

Plate 6.7, Figs. 9–11.

Spore, monad, shape oblate, outline elliptic in equatorial view, polar axis 15 µm, equatorial diameter 23 µm under SEM, 18 µm and 27 µm under LM, monolete, laesurae 17 µm long, spore wall 0.8–1.5 µm thick, thickest in distal area (LM), sculpture on distal side verrucate, proximal side microverrucate, fossulate (SEM).

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

**Polypodiaceae, gen. et spec. indet. 5** **P**

Plate 6.7, Figs. 12–14.

Spore, monad, shape oblate, outline elliptic in equatorial view, equatorial diameter 22 µm, polar axis 16 µm under SEM, 27 µm and 19 µm under LM, monolete, laesurae 12 µm long (LM), spore wall 2.3 µm thick (LM), sculpture rugulate to verrucate.

Occurrence: 10 Ma sedimentary rock formation at Tröllatunga.

**Polypodiaceae, gen. et spec. indet. 6** **P**

Plate 7.4, Figs. 1–3; Plate 8.2, Figs. 2–4; Plate 10.5, Figs. 4–6.

Spore, monad, shape oblate, outline elliptic in equatorial view, equatorial diameter 50–65 µm, polar axis 36–52 µm under SEM, 65–85 µm and 43–61 µm under LM, monolete, laesurae 18 µm long, sculpture rugulate, fossulate (SEM).

*Occurre*nce: 9–3.8 Ma sedimentary rock formations at Hrútagil (9–8 Ma), Hestabrekkur (7–6 Ma) and Tjörnes (Reká, Skeifá; 4.2–3.8 Ma).

**Polypodiaceae gen. et spec. indet. 7** **P**

Plate 9.3, Figs. 4–6.

Spore, monad, shape oblate, outline elliptic in equatorial view, polar axis 20–22 µm, equatorial diameter 27–34 µm under SEM, 21–25 µm and 31–41 µm under LM, monolete, spore wall (exospore) 1.6–2.2 µm thick (LM), sculpture on distal side rugulate, fossulate, proximal side perforate (SEM).

Occurrence: 5.5 Ma sedimentary rock formation at Selárgil.

**Polypodiaceae gen. et spec. indet. 8** **P**

Plate 9.3, Figs. 7–9.

Spore, monad, shape oblate, outline elliptic in equatorial view, polar axis 33 μm, equatorial diameter 44 μm under SEM, 36 μm and 56 μm under LM, monolete, spore wall (exospore) 1.6–2.2 μm thick (LM), sculpture on distal side verrucate, verrucae on distal side much larger than centrally on proximal side (SEM).

*Occurrence*: 5.5 Ma sedimentary rock formation at Selárgil.

**Polypodiaceae gen. et spec. indet. A** **M**

Plate 11.32, Figs. 1–2.

Frond, preserved part 3.0 cm long, 2.0 cm at its widest part, pinnately compound, pinnae 4–12 mm long, 3–4 mm wide at base, tapering towards apex, pinnae lobed, degree of lobation one-third to two-thirds of width of pinna, pinnulae alternate, veins in pinnulae sinuous, sending off lateral veins that curve towards the apex, pinnulae entire margined, 1–3.5 mm long, 1–1.5 mm wide, widest at base, shape variable, basalmost pinnula markedly wider than remaining pinnulae, much longer on apical side, pinnulae decreasing in size towards apex of pinna, apex of pinnulae obtuse, rounded or retuse.

*Occurrence*: 0.8 Ma sedimentary rock formation at Svínafell.

**Pteridophyta gen. et spec. indet 1** **M**

Plate 6.6, Figs. 6–7.

2005 Pteridophyta gen. et spec. indet. 1 – Denk et al.: p. 373, figs. 10–11.

Leaf fragment, 1.4 cm long, probably representing a small medial part of a pinna, only two pairs of alternate segments preserved, ca 7 mm long and ca 3 mm wide, narrow oblong, margin entire, bluntly rounded at the apex, fused for 2 mm from the rhachis, sinus narrow and sharp, primary vein almost perpendicular to the rhachilla, secondaries very thin, indistinct.

*Occurrence*: 10 Ma sedimentary rock formation at Húsavíkurkleif.

**Incertae sedis – unassigned spores**

**Monolete spore, fam., gen. et spec. indet 1** **P**

Plate 7.4, Figs. 4–6.

Spore, monad, shape oblate, outline subcircular in polar view, equatorial diameter 55–58 μm under SEM, 55–60 μm under LM, monolete, laesura 31 μm long (SEM), spore wall (exospore) 1.5 μm thick (LM), surface psilate (SEM).

*Occurrence*: 9–8 Ma sedimentary rock formation at Hrútagil.

**Monolete spore, fam., gen. et spec. indet 2** **P**

Plate 7.4, Figs. 7–12.

Spore, monad, shape oblate, outline subcircular-elliptic in polar view, equatorial diameter 18–21 × 26 µm under SEM, 18–23 × 26–27 µm under LM, monolete, laesurae 15 µm long (SEM), spore wall (exospore) 1.5 µm thick (LM), sculpture on distal side verrucate to rugulate, fossulate, proximal side verrucate to rugulate, leasurae densely covered by distinct, small verrucae and rugulae (SEM).

*Occurrence*: 9–8 Ma sedimentary rock formation at Hrútagil.

**Monolete spore, fam., gen. et spec. indet 3** **P**

Plate 10.6, Figs. 4–6.

Spore, monad, shape oblate, outline subcircular-elliptic in polar view, equatorial diameter 26×30 µm under SEM, 30×36 µm under LM, monolete, laesurae 22 µm long (LM), spore wall (exospore) 1.4 µm thick (LM), sculpture microverrucate (SEM).

*Occurrence*: 4.3–4.2 Ma sedimentary rock formation at Tjörnes (Egilsgjóta).

**Monolete spore, fam., gen. et spec. indet 4 (Polypodiaceae)** **P**

Plate 10.6, Figs. 7–12.

Spore, monad, shape oblate, outline elliptic in polar view, polar axis 17–29 µm, equatorial diameter 21–42 µm under SEM, 17–32 µm and 25–52 µm under LM, monolete, laesurae 12–21 µm (SEM), 21–25 µm (LM); spore wall (exospore) 2.5–3.3 µm thick (LM), sculpture on distal side rugulate verrucate with interspersed small verrucae, proximal side microverrucate (SEM).

*Occurrence*: 4.3–3.8 Ma sedimentary rock formations at Tjörnes (Egilsgjóta, Reká, Skeifá).

**Trilete spore, fam., gen. et spec. indet. 1** **P**

Plate 5.2, Figs. 1–3.

Spore, monad, shape oblate, outline triangular in polar view, equatorial diameter 31–32 µm under SEM, 35–38 µm under LM, trilete, spore wall (exospore) 0.7–1 µm thick (LM), surface psilate (SEM).

*Occurrence*: 12–6 Ma sedimentary rock formations at Surtarbrandsgil and Brekkuá (7-6 Ma).

**Trilete spore, fam., gen. et spec. indet. 2** **P**

Plate 9.3, Figs. 10–12.

Spore, monad, shape oblate, outline rounded triangular in polar view, equatorial diameter 37–41 μm under SEM, 40–42 μm under LM, trilete, laesurae 18–19 μm long (LM); spore wall (exospore) 1.7–1.8 μm thick (LM), sculpture rugulate with a microechinate to granulate suprasculpture (SEM).

*Occurrence*: 5.5 Ma sedimentary rock formation at Selárgil.

**Trilete spore, fam., gen. et spec. indet. 3** **P**

Plate 10.5, Figs. 7–9.

Spore, monad, shape oblate, outline rounded triangular in polar view, equatorial diameter 74–76 μm under SEM, 85–87 μm under LM, trilete, laesurae 27–37 μm long (LM); spore wall (exospore) 4.5–5 μm thick, sculpture on proximal side prominently verrucate, with a granulate suprasculpture (SEM).

*Occurrence*: 4.3–4.2 Ma sedimentary rock formation at Tjörnes (Egilsgjóta).

**Trilete spore, fam., gen. et spec. indet. 4** **P**

Plate 10.5, Figs. 10–12.

Spore, monad, shape oblate, outline circular in polar view, equatorial diameter 26–29 μm under SEM, 37–38 μm under LM, trilete, laesurae 8.5 μm long (SEM); spore wall (exospore) 1.2–1.8 μm thick (LM), sculpture verrucate (SEM).

*Occurrence*: 4.3–4.2 Ma sedimentary rock formation at Tjörnes (Egilsgjóta).

**Trilete spore, fam., gen. et spec. indet. 5** **P**

Plate 10.6, Figs. 1–3.

Spore, monad, shape oblate, outline rounded triangular in polar view, equatorial diameter 45–50 μm under SEM, 55–58 μm under LM, trilete, laesurae 9 μm long (SEM); spore wall (exospore) 1.5–1.8 μm thick (LM), sculpture slightly verrucate with a granulate suprasculpture (SEM).

*Occurrence*: 3.9–3.8 Ma sedimentary rock formation at Tjörnes (Skeifá).

**Trilete spore, fam., gen. et spec. indet. 6** **P**

Plate 11.3, Figs. 7–9.

Spore, monad, shape oblate, outline rounded triangular in polar view, polar axis ca 12 μm, equatorial diameter ca 15 μm under SEM, ca 13 μm and ca 18 μm under

LM, trilete; spore wall (exospore) 0.8–1.3 μm thick (LM), sculpture verrucate with a granulate suprasculpture (SEM).

*Occurrence*: 1.7 Ma sedimentary rock formation at Bakkabrúnir.

**Trilete spore, fam., gen. et spec. indet. 7** **P**

Plate 11.3, Figs. 10–12.

Spore, monad, shape oblate, outline rounded triangular in polar view, diameter 33–34 μm under SEM, 35–36 μm under LM, trilete; laesurae 12–13 μm (LM), spore wall (exospore) 3.3–4.1 μm thick (LM), sculpture areolate, fossulate, areolae convex, in some cases collapsed (SEM).

*Occurrence*: 1.7 Ma sedimentary rock formation at Bakkabrúnir.

**Trilete spore, fam., gen. et spec. indet. 8** **P**

Plate 11.17, Figs. 4–6.

Spore, monad, shape oblate, outline rounded triangular in polar view, diameter 11–13 μm under SEM, 15–20 μm in LM, trilete, spore wall (exospore) 0.8–1.2 μm thick (LM), surface sculpture verrucate, fossulate (SEM).

*Occurrence*: 1.1 Ma sedimentary rock formation at Stöð.

**Trilete spore, fam., gen. et spec. indet. 9 (*Botrychium* sp.)** **P**

Plate 11.31, Figs. 10–12.

Spore, monad, shape oblate, outline rounded triangular in polar view, diameter 28–34 μm under SEM, 36–37 μm under in LM, trilete; spore wall (exospore) 1.6–1.7 μm thick (LM), sculpture verrucate to rugulate, granulate, with microverrucate suprasculpture, sculpture less distinct next to laesurae (SEM).

*Occurrence*: 0.8 Ma sedimentary rock formation at Svínafell.

## 3.4 Gnetophyta

### Ephedraceae

***Ephedra* sp.** **P**

Plate 5.3, Figs. 1–6.

Pollen, monad, shape oblate, outline narrow elliptic in equatorial view, polar axis 17–19 μm, equatorial diameter 32–35 μm under SEM, 21–22 μm and 36–38 μm

under LM, inaperturate, polyplicate, four to six plicae, area between plicae 6–9 μm wide, sculpture fossulate, areas between fossulae irregularly polygonal, plicae psilate (SEM).

*Occurrence*: 12 Ma sedimentary rock formation at Surtarbrandsgil.

## 3.5 Ginkgophyta

### Ginkgoaceae

#### *Ginkgo* sp.

Plate 6.8, Figs. 1–3.

Pollen, monad, shape spheroidal, outline subcircular in polar view (SEM), monosulcate, outline of a collapsed grain elliptic in equatorial view (LM), equatorial diameter 22.6–24.5 μm (SEM), sculpture rugulate to microrugulate, rugulae in some cases fused.

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

## 3.6 Pinophyta

### Cupressaceae (incl. Taxodiaceae)

#### *Cryptomeria anglica* Boulter M

Plate 5.4, Figs. 1–5.

1859 *Araucarites sternbergii* Goepp. – Heer: pp. 316, 317.
1868 *Sequoia sternbergii* (Goepp.) Heer – Heer: p. 140, pl. 24, figs. 7–10.
1886 *Sequoia sternbergii* (Goepp.) Heer – Windisch: p. 28.
1966 *Sequoia sternbergii* (Goepp.) Heer – Friedrich: p. 63, pl. 1, figs. 5, 7.
1978 *Sequoia sternbergii* (Goepp.) Heer – Akhmetiev et al.: p. 177, pl. 1, figs. 1, 4, 8, 14.
1981 Sequoioideae – Friedrich and Símonarson: fig. 8.
1984 *Brjanslaekuria kryshtofovichii* Sveshnikova – Sveshnikova: p. 264, pl. 1, figs. 1–4, pl. 2, figs. 1–2.
2005 *Cryptomeria anglica* Boulter – Denk et al.: p. 378, figs. 45–49.
2008a *Cryptomeria anglica* Boulter – Grímsson and Símonarson: fig. 16.

Sterile foliage shoots with helically disposed falcate needle leaves, usually patent, rarely appressed, with blunt apex and long decurrent base, leaves around 1.0 cm long, quadrangular in cross-section, with lateral margin indicated as a line running parallel with and close to the adaxial edge of needles, amphistomatic.

Cuticle of medium thickness, showing quadrangular more or less elongate cells and two stomatal bands; stomata incompletely amphicyclic, densely arranged and irregularly oriented, roundish, 50–58 μm long, with a simple circle of subsidiary cells bordered by a faintly thicker peripheral line, guard cells forming distinct cuticular thickenings at their polar ends (= T-pieces).

*Occurrence*: 12 Ma sedimentary rock formation at Surtarbrandsgil.

*Remarks*: The stomatal topography and structure of the needles studied unequivocally refer to *Cryptomeria* (Ma et al. 2007). Stomata in *Sequoia* and *Sequoiadendron* are fully amphicyclic with an inner circle of thicker subsidiary cells. The European records of *Cryptomeria* have been assigned to two more or less morphological species. *Cryptomeria rhenana* Kilpper (1968; Miocene of Rhineland) is based on a seed cone, whereas *C. anglica* Boulter (1969) and Boulter and Chaloner (1970; Neogene of Derbyshire) is defined on anatomically preserved foliage shoots. Sterile remains from both localities match well those from Iceland in morphology and cuticle structure. We follow the interpretation of Kilpper (1968) who did not directly assign the sterile foliage shoots to *C. rhenana*, although it may seem to be very formal. Similar shoots of *Doliostrobus* (now *D. taxiformis* var. *sternbergii* – see Kvaček 2002) differ in having completely amphicyclic stomata with narrow subsidiary cells and distinct crystal cavities in the cuticle. The occurrence of *Cryptomeria* in the Miocene of Iceland is the westernmost record of this genus stressing the palaeofloristic connection of Iceland with the rest of Europe during the Neogene. The single extant species, *Cryptomeria japonica* (L. f.) D. Don., is native to Japan.

### *Glyptostrobus europaeus* (Brongn.) Unger M

Plate 4.4, Figs. 7–11.

2007a Cupressaceae gen. et spec. indet. – Grímsson et al.: p. 187, pl. 1, figs. 1–3.
2007a *Glyptostrobus europaeus* (Brongn.) Unger – Grímsson et al. : p. 187, pl. 2, figs. 1–11.
2007b Cupressaceae gen. et spec. indet. – Grímsson et al. : fig. 2, a–b.
2007b *Glyptostrobus europaeus* (Brongn.) Unger – Grímsson et al.: fig. 2, d–h.
2008a *Glyptostrobus europaeus* (Brongn.) Unger – Grímsson and Símonarson: fig. 8.

Leaves polymorphic on different shoot types; (1) vegetative elongated shoots >5 cm long, leaves spirally arranged, blade spreading and curved towards axis distally, narrow and long, 5–10 mm long, widest at point of insertion, apex acute, base adnate; (2) vegetative short shoots, branched, branches >3 cm long, leaves spirally arranged, appearing subopposite, scale-like, blades spreading, short and wide, 2–6 mm long, keeled with convex abaxial and concave adaxial surfaces, apex acute, base adnate; (3) vegetative shoots with flattened axes, branching restricted to a single plane, branches bearing small, simple, scale-like leaves, leaves decussately arranged, facial leaves hard to distinguish (due to compression), small and

appressed, flanked by marginal leaves, marginal leaves consisting of an adnate base and a free portion, free portion overlapping part of base of subsequent leaves.

Stomata amphicyclic, 65–80 μm long, with elliptic pit 26–35 μm long and 14–21 μm wide, subsidiary cells narrow, stomata scattered, arranged in groups or short rows. Dimensions, arrangement, and orientation of stomata matching the modern *G. pensilis*.

Cones inverted pear-shaped, stalked, stalk 1.7 to >2.4 cm long, 2.5–3.5 mm wide, cones in clusters of two and more, 1.9–2.3 cm long, 1.7–1.8 cm wide, length to width ratio 1.19–1.32, wide obovate; > 16 scales per cone; scales 9–22 mm long, narrow at base and widest at their distal margin, narrow obovate, with distinct umbo at central upper part.

*Occurrence*: 15 Ma sedimentary rock formation at Botn.

*Remarks*: The genus has an extensive fossil record in the Cainozoic of the Northern Hemisphere (Mai 1995; Budantsev 1997; Manchester 1999). *Glyptostrobus* includes only one extant species restricted to Southeast Asia. Branch dimorphism typical of modern *Glyptostrobus* is also encountered in the fossil material. The three shoot types recognized here for fossil material have been termed "taxodioid", "cryptomerioid", and "cupressoid" by Henry (Henry and McIntyre 1926 cited in Florin 1931, pp. 163–164). The fossil and the modern species are very similar in morphology of vegetative and reproductive structures.

### ***Sequoia abietina* (Brongn.) Knobl.** **M**

Plate 4.5, Figs. 5–8.

1988 *Metasequoia occidentalis* Chaney – Símonarson: p. 24, fig. 2.
2007a *Sequoia abietina* (Brongn.) Knobl. – Grímsson et al.: p. 187, pl. 3–4.
2007b *Sequoia abietina* (Brongn.) Knobl. – Grímsson et al.: fig. 2, i–o.

Branchlets >75 mm long, 1.7–2.9 cm wide, axis 1–3 mm wide; leaves arranged spirally, appearing irregularly distichous, three to five leaves per 1 cm axis; leaf apex acute, base adnate, forming a ridge running parallel to the axis; lamina 9–20 mm long, 1.3–3.1 mm wide, length to width ratio 5.5–7.7, diverging from axis at angles of 35–65°, base of lamina asymmetrical, twisting at insertion to axis; leaf bifacially flattened, abaxial surface with strong median vein appearing as low ridge, lateral faces planar or slightly concave, adaxial surface not keeled, planar or slightly convex, midvein clearly visible in proximal part, less visible in apical part, margin entire.

Epidermis in non-stomatal condition composed of narrow elongate, rectangular or spindle-shaped cells with straight margins, 12–15 μm wide and 60–130 μm long; epidermal cells between stomata broad rectangular to elongate; stomata aligned parallel to the midvein and arranged in rows that form bands, number of subsidiary cells varying from 4 (two polar and two lateral subsidiary cells) to >4 (with additional lateral subsidiary cells); stomata 39–44 μm long.

*Occurrence*: 15 Ma sedimentary rock formation at Botn.

*Remarks*: Today *Sequoia* incorporates the single species *S. sempervirens* (Lamb.) Endl. that has a relictual distribution in western North America. The fossil record of *Sequoia* extends back to the Palaeogene and indicates a vast northern hemispheric distribution of the genus during large parts of the Cainozoic. In Europe, *S. abietina* is the only species recognized on the basis of leaf fossils (Knobloch 1969). Similar branches from the Cainozoic of North America have been described as *S. affinis* Lesqu. (Chaney 1951; Chaney and Axelrod 1959; Meyer and Manchester 1997).

**Cupressaceae gen. et spec. indet. 1 (*Cryptomeria* sp.)** **P**

Plate 4.3, Figs. 1–3.

Pollen, monad, shape spheroidal, outline circular, diameter 27–30 μm under SEM, 31–35 μm under LM, leptoma on distal side with a papilla, pollen wall 0.8 μm thick (LM), sculpture scabrate (LM), microverrucate with a microechinate suprasculpture (SEM), microverrucae 0.5–8 μm, orbiculae few, <0.5 μm in diameter.

*Occurrence*: 15 Ma sedimentary rock formation at Botn.

**Cupressaceae gen. et spec. indet. 2 (*Glyptostrobus* sp.)** **P**

Plate 4.4, Figs. 1–6; Plate 5.3, Figs. 7–14.

Pollen, monad, shape spheroidal, outline circular, often ruptured and with fissurae, diameter 27–28 μm under SEM, 31–32 μm under LM, leptoma on distal side with a papilla, pollen wall 1–1.5 μm thick (LM), sculpture scabrate (LM), verrucate to rugulate with a microverrucate suprasculpture, cauliflower-like (SEM), sculpture in leptoma region with low relief, orbiculae confined mostly to leptoma area (SEM).

*Occurrence*: 15–12 Ma sedimentary rock formations at Botn (15 Ma) and Surtarbrandsgil (12 Ma).

**Cupressaceae gen. et spec. indet. 3 (*Juniperus* sp.)** **P**

Plate 4.3, Figs. 4–13.

Pollen, monad, shape spheroidal, outline circular, diameter 18–29 μm under SEM, 23–35 μm under LM, ulcerate, pollen wall 0.6–1.1 μm thick (LM), sculpture more or less psilate (LM), microverrucate, echinate to granulate (SEM), granula ≤0.3 μm, leptoma granulate, orbiculae microechinate, sparsely distributed, ca 0.5 μm in diameter (SEM).

*Occurrence*: 15 Ma sedimentary rock formation at Botn.

**Cupressaceae gen. et spec. indet. 4 (*Sequoia* sp.)** **P**

Plate 4.5, Figs. 1–4.

Pollen, monad, shape spheroidal, outline circular, diameter 21–24.1 μm under SEM, 23–28 μm under LM, leptoma with papilla, pollen wall ca 1.2 μm thick (LM), sculpture scabrate (LM), rugulate with microechinate to granulate suprasculpture (SEM), leptoma sparsely covered with orbiculae, leptoma area circular, ca 14 μm in diameter, papilla 4.1–4.8 μm long and 2–3 μm wide (SEM).

*Occurrence*: 15–12 Ma sedimentary rock formations at Botn (15 Ma) and Surtarbrandsgil (12 Ma).

## Pinaceae

***Abies steenstrupiana* (Heer) Friedrich** **M**

Plate 5.4, Figs. 6–9; Plate 8.3, Figs. 1–11; Plate 9.4, Fig. 5.

1859 *Pinus steenstrupiana* Heer – Heer: p. 318.
1868 *Pinus steenstrupiana* Heer – Heer: p. 144, pl. 24, figs. 23–25, (?) 26.
1975 *Abies* – Sigurðsson: fig. 8.
1886 *Pinus steenstrupiana* Heer – Windisch: p. 29.
1966 *Abies steenstrupiana* (Heer) Friedrich – Friedrich: p. 58, pl. 1, figs. 6, 9, 10, text-fig. 13.
2005 *Abies steenstrupiana* (Heer) Friedrich – Denk et al.: p. 373, figs. 14–18.

Cone scales, winged seeds, and leaves; scales broad flabelliform, base decurrent, 1.4–2.8 cm long and 1.5–3.4 cm wide, with distinct radial striae, no bracts visible on dorsal parts of scales; seeds broadly winged, 1.0–1.7 cm long; wing attached to almost half the circumference of the seed, 5.7–11 mm wide, widest at its distal end, seed roundish to elliptic, 3–10 mm long and 2–5.8 wide; leaves flat needles, linear, 1–2.5 cm long, 1.2–2.4 mm wide, oblong, apex commonly notched, slightly twisted at base, with widened roundish area of attachment.

*Occurrence*: 12–5.5 Ma sedimentary rock formations at Surtarbrandsgil (12 Ma), Langavatnsdalur, Þrimilsdalur, Hestabrekkur, Brekkuá, Stafholt (7–6 Ma) and Selárgil (5.5 Ma).

***Abies* sp.** **P**

Plate 9.5, Figs. 1–3; Plate 10.7, Figs. 1–3.

Pollen, monad, shape oblate, elliptic in equatorial view, bisaccate, corpus with a markedly thickened cappa (*Abies* crest), sacci subspherical, attachment to corpus short, 40–45 μm in diameter, equatorial diameter 90–165 μm (SEM), 105–175 μm (LM), polar axis 70–100 μm long (SEM), 70–105 μm (LM), cappa surface sculpture rugulate to verrucate, perforate, fossulate.

*Occurrence*: 12–3.8 Ma sedimentary rock formations at Surtarbrandsgil (12), Tröllatunga, Húsavíkurkleif (10 Ma), Hrútagil (9–8 Ma), Hestabrekkur (7–6 Ma), Selárgil (5.5 Ma) and Tjörnes (Egilsgjóta, Reká, Skeifá; 4.3–3.8 Ma).

*Remarks:* The variability of *Abies* pollen observed in the Icelandic sediments most likely represents more than a single natural species. Relatively bad preservation makes it difficult to distinguish between individual species.

### *Cathaya* sp. A. M

Plate 5.5, Figs. 4–9.

Isolated leaf fragments, 1.5 to >3 cm long, midvein prominent; hypostomatic, adaxial epidermis with elongate rectangular epidermal cells with smooth anticlinal walls, epidermal cells 60–140 μm long; abaxial epidermis with bands of stomata; stomata oriented along long axis of leaf, stomata with one or two lateral subsidiary cells on each side and with one polar subsidiary cell, polar cells shared between adjacent stomata, stomata 40–50 μm long; subsidiary cells with smooth anticlinal walls.

*Occurrence*: 12 Ma sedimentary rock formation at Surtarbrandsgil (12 Ma).

### *Cathaya* sp. P

Plate 4.6, Figs. 1–3; Plate 9.5, Fig. 5.

Pollen, monad, shape oblate, elliptic in polar view, bisaccate, sacci half-spherical, broadly attached to corpus (LM), polar axis 50–55 μm long, equatorial axis 65–70 μm long under SEM, 55–60 μm and 70–80 μm long under LM, leptoma, sculpture of sacci microechinate, perforate (SEM).

*Occurrence*: 15–5.5 Ma sedimentary rock formations at Botn (15 Ma), Surtarbrandsgil (12 Ma) and Selárgil (5.5 Ma).

*Remarks*: Pollen of Tertiary *Cathaya* has been described and figured among others by Liu and Basinger (2000) and Saito et al. (2000).

### *Larix* sp. M

Plate 6.8, Figs. 4–6 ; Plate 10.2, Figs. 5–7.

1978 *Larix* sp.1 – Akhmetiev et al.: p. 180, pl. 12, fig. 17.
1978 *Larix* sp.2 – Akhmetiev et al.: p. 180, pl. 12, fig. 21.
1978 *Laxis* sp. – Akhmetiev et al.: p. 181, pl. 13, fig. 16.
2005 *Larix* sp. – Denk et al.: p. 375, figs. 19–22.

Long shoots with short, lateral spur shoots; small protrusions on long shoots indicating the position of abscised leaves on long shoots; needle leaves narrow and linear, in bundles, 2.1–2.9 cm long, 0.4–0.6 mm wide.

Cones, elliptic in outline, 1.6 cm long, 8.5–9.5 mm wide, on short peduncle, peduncle upto 3.5 mm long, cone composed of few spirally arranged scales that are 4.5–5.5 mm wide, apical part of scale round with smooth margin.

*Occurrence*: 10–3.8 Ma sedimentary rock formations at Tröllatunga (10 Ma), Hestabrekkur, Brekkuá (7–6 Ma) and Tjörnes (Skeifá, 3.9–3.8 Ma).

*Remarks*: The record in the Miocene of Iceland may either be connected with many others in the Canadian Arctic Miocene (LePage and Basinger 1991) or with those in Siberia because *Larix* did not reach Central Europe prior to the Pliocene (Mai 1995).

### ***Picea* sect. *Picea* sp.** **M**

Plate 5.6, Figs. 1–7; Plate 6.9, Figs. 3–8; Plate 7.5, Fig. 4; Plate 9.4, Fig. 6; Plate 10.2, Fig. 4.

1859 *Pinus aemula* Heer – Heer: p. 318.
1859 *Pinus brachyptera* Heer – Heer: p. 318.
1868 *Pinus microsperma* Heer – Heer: p. 142, pl. 24, figs. 11–17.
1868 *Pinus aemula* Heer – Heer: p. 143, pl. 24, fig. 20.
1868 *Pinus brachyptera* Heer – Heer: p. 143, pl. 24, fig. 18.
1886 *Pinus brachyptera* Heer – Windisch: p. 30.
1954 *Picea* sp. – Áskelsson: p. 94, fig. 3.
1966 *Picea microsperma* (Heer) Friedrich – Friedrich: p. 60, pl. 1, fig. 11.
1978 *Picea* sp. 1 – Akhmetiev et al.: p. 177, pl. 2, fig. 5.
1978 *Picea* sp. 2 – Akhmetiev et al.: p. 177, pl. 2, figs. 9, 11.
1978 *Picea breweriana* Wats. *fossilis* – Akhmetiev et al.: p. 177, pl. 2, figs. 6, 7.
1978 *Picea* sp. – Akhmetiev et al.: pp. 178–180, pl. 7, fig. 6, pl. 8, fig. 4, pl. 9, fig. 1, pl. 12, figs. 1–6, 9, 11, 15, 18, pl. 13, fig. 12.
2005 *Picea* sect. *Picea* sp. – Denk et al.: p. 375, figs. 23–33.
2007a cf. *Picea* sp. – Grímsson et al.: p. 186, pl. 1, fig. 4.
2007b *Picea* sp. – Grímsson et al.: fig. 2, c.

Pollen cone with *Picea* type pollen *in situ*, seed cones, winged seeds, and leaves; pollen cone about 2.5 cm long, in late stage of maturity, with microsporophylls widely spaced, bisaccate pollen 61×40 μm; seed cones maximal 9.0 cm long and 2.5 cm wide, seed scales closely imbricate, distal margin entire, ca 1.1 cm wide; winged seeds 1.6–2.2 cm long, 4–7.6 mm wide, wing attached to distal part of seed; isolated leaves 1.1 to >3 cm long, 0.9–1.2 mm wide, grooved, with a median midrib, apex acute, base truncate.

*Occurrence*: 15–3.8 Ma sedimentary rock formations at Selárdalur (15 Ma), Surtarbrandsgil (12 Ma), Tröllatunga (10 Ma), Tindafjall, Hrútagil (9–8 Ma), Þrimilsdalur, Hestabrekkur, Brekkuá, Stafholt, Vindfell (7–6 Ma), Selárgil (5.5 Ma) and Tjörnes (Kaldakvísl, Skeifá; 4.4–3.8 Ma).

*Remarks*: Examination of living species of *Picea* shows that the fossils are very similar to several North American species having entire-margined rounded apices of the woody cone scales, but also to northern populations of the European *P. abies* (L.) Karsten (*P. abies* subsp. *obovata* Ledeb.), and to at least ten East Asian species

belonging to the section *Picea*. Seed cones, pollen cones, winged seeds, and leaves are referred to this entity, which may represent more than one natural species.

***Picea* sp.** **P**

Plate 5.6, Figs. 8–10; Plate 6.10, Figs. 1–5, 8; Plate, 7.5, Figs. 5–7; Plate 10.7, Figs. 4–6.

Pollen, monad, shape oblate, bisaccate, pollen sacs broadly attached to corpus, half-spherical, polar axis 58–83 μm, equatorial axis 78–121 μm under SEM, 64–115 μm and 87–160 μm under LM, diameter of sacci 35–65 μm under LM; leptoma; pollen sacs microverrucate, cappa microverrucate, cappula (leptoma) with verrucate thickenings.

*Occurrence*: 12–3.8 Ma sedimentary rock formations at Surtarbrandsgil (12 Ma), Tröllatunga, Húsavíkurkleif (10 Ma), Hrútagil (9–8 Ma), Hestabrekkur (7–6 Ma), Selárgil (5.5 Ma) and Tjörnes (Egilsgjóta, Reká, Skeifá; 4.3–3.8 Ma).

***Pinus* sp.** **M**

Plate 8.4, Figs. 5–7.

1868 *Pinus thulensis* Steenstrup – Heer: p. 141, pl. 24, fig. 21.
2005 cf. *Pinus* sp. – Denk et al.: p. 377, fig. 34.

Winged seeds, 2.2 cm long, seed elliptic, 5.2 mm long and 0.34 mm wide, attached to the wing along half its circumference, wing asymmetrical. Leaves narrow, long, in fascicles of two.

*Occurrence*: 7–6 Ma sedimentary rock formation at Þrimilsdalur.

***Pinus* sp. 1 (Diploxylon type)** **P**

Plates 4.6, Figs. 4–7, Plate 6.10, Figs. 9–12; Plate 7.5, Figs. 8–11; Plate 8.4, Figs. 1–3; Plate 9.5, Fig. 4; Plate 10.7, Fig. 7; Plate 11.4, Figs. 1–6; Plate 11.17, Figs. 7–9; Plate 11.33, Figs. 1–3.

Pollen, monad, shape oblate, elliptic in polar view, bisaccate, sacci subspherical, sacci narrowly attached to corpus, equatorial diameter 40–70 μm under SEM, 40–83 μm under LM, saccus diameter 20–40 μm under SEM, 20–55 μm under LM, leptoma, sculpture of cappa surface rugulate, verrucate, fossulate, with a granulate suprasculpture; sacci perforate (SEM).

*Occurrence*: 15–0.8 Ma sedimentary rock formation at Botn (15 Ma), Surtarbrandsgil (12 Ma), Tröllatunga, Húsavíkurkleif (10 Ma), Hrútagil (9–8 Ma), Hestabrekkur (7–6 Ma), Selárgil (5.5 Ma), Tjörnes (Egilsgjóta, Reká, Skeifá; 4.3–3.8 Ma), Bakkabrúnir (1.7 Ma), Stöð (1.1 Ma) and Svínafell (0.8 Ma).

*Remarks*: Great morphological variability encountered within pollen assigned to *Pinus* Diploxylon suggests that this morphotype may represent various biological

species. Diploxylon pines belong to subgenus *Pinus* and comprise ca 70 species across the Northern Hemisphere (The Gymnosperm Database 2010).

### *Pinus* sp. 2 (Haploxylon type) P

Plate 7.6, Figs. 1–3

Pollen, monad, shape oblate, elliptical in polar view, bisaccate, sacci half-spherical, sacci broadly attached, area of attachment 30 µm wide, equatorial diameter ca 66 µm, polar axis ca 45 µm under SEM, ca 75 µm and 47 µm under LM, diameter of sacci ca 30 µm under LM; leptoma; sculpture of cappa rugulate, verrucate, fossulate, perforate (SEM).

*Occurrence*: 9–8 Ma sedimentary rock formations at Hrútagil.

*Remarks*: Pollen of the Haploxylon type is found in *Pinus* subgenus *Strobus* that comprises ca 44 spp. with a northern hemispheric distribution (The Gymnosperm Database 2010). Matthews and Ovenden (1990) reported five-needled pines of subsection *Cembrae* with affinities to East Asian species for the Late Tertiary of Arctic North America.

### *Pseudotsuga* sp. M

Plate 6.8, Fig. 7; Plate 8.4, Figs. 8–9.

2005 *Pseudotsuga* sp. – Denk et al.: p. 377, fig. 35–36.

Seed cone, 5.6 cm long and 3.8 cm wide measured from the distal ends of the bracts, 2.36 cm wide measured from the distal ends of the cone scales; peduncle 8.2 mm long and 3.4 mm wide, attached to cone at an acute angle; cone length to width ratio 1.5 when bracts are included in measurement, 2.4 when bracts are not measured, cone oblong cylindrical; cone scales relatively long with smoothly rounded distal margin and wedge shaped proximally, distal region of scales commonly asymmetrical, scales much shorter than their bracts, outer surface of scales marked by fine cellular rows radiating from the proximal part towards the distal margin; three-pronged bracts projecting like tongues and pointing straight towards tip of the scales, bracts extend beyond the distal scale margin, bracts long acute-tipped with lateral wing-like extensions in their lower parts.

*Occurrence*: 10–6 Ma sedimentary rock formations at Tröllatunga (10 Ma), Hrútagil (9–8 Ma) and Þrimilsdalur (7–6 Ma).

*Remarks*: The distinctive form of the bracts is characteristic of *Pseudotsuga*. The fossil record of this genus in Europe is restricted to a few uncertain leaf remains and no records of cones belonging to *Pseudotsuga* are known from the Cainozoic of Europe (Mai 1995). The oldest macrofossil record in North America is from the early Oligocene of Oregon (Schorn and Erwin 2000). By the Miocene, the genus was also present in Japan. *Pseudotsuga* consists of eight (to nine) extant species displaying an East Asian-western North American disjunct distribution.

***Larix/Pseudotsuga* sp.** **P**

Plate 6.8, Figs. 8–10; Plate 7.5, Figs. 1–3; Plate 9.5, Figs. 6–8; Plate 10.8, Figs. 1–3.

Pollen, monad, shape spheroidal, outline circular, 52–86×53–89 µm under SEM, 53–97×53–107 µm under LM, inaperturate, in some cases Y-shaped impression mark visible, tectate, sculpture microverrucate with a granulate suprasculpture (SEM).

*Occurrence*: 10–3.8 Ma sedimentary rock formations at Tröllatunga, Húsavíkurkleif (10 Ma), Hrútagil (9–8 Ma), Selárgil (5.5 Ma) and Tjörnes (Egilsgjóta, Reká, Skeifá; 4.3–3.8 Ma).

***Tsuga* sp.** **M**

Plate 5.7, Figs. 4–8; Plate 8.4, Figs. 10–12.

2005 *Tsuga* sp. – Denk et al.: p. 377, figs. 37–40.

Flat needle leaves, shortly petiolate or incomplete at base, hypostomatic with cells longitudinally oriented, narrow elongate, straight–walled. Stomata in narrow bands, longitudinally oriented, 48–52 µm long, incompletely amphicyclic, with two (short) lateral subsidiary cells and two polar, slightly elongate cells.

*Occurrence*: 12–6 Ma sedimentary rock formations at Surtarbrandsgil (12 Ma), Fífudalur, and Þrimilsdalur (7–6 Ma).

***Tsuga* sp. 1 (*Tsuga diversifolia* type)** **P**

Plate 4.6, Figs. 8–10; Plate 5.7, Figs. 9–11; Plate 6.11, Figs. 1–3; Plate 7.7, Figs. 1–4; Plate 10.8, Figs. 4–8.

Pollen, monad, shape oblate, monosaccate, outline circular in polar view, equatorial diameter 30–80 µm under SEM, 32–92 µm under LM, leptoma; monosaccus relatively wide, coarsely radially folded, surface echinate; tectate, sculpture rugulate to verrucate with echinate suprasculpture, rugulae and verrucae less distinct in leptoma area (SEM).

*Occurrence*: 15–4.0 Ma sedimentary rock formations at Botn (15 Ma), Surtarbrandsgil (12 Ma), Húsavíkurkleif (10 Ma), Hrútagil (9–8 Ma) and Tjörnes (Reká, 4.2–4.0 Ma).

*Remarks*: See Sivak (1978) for a comprehensive treatment of modern and fossil pollen of *Tsuga*.

***Tsuga* sp. 2** **P**

Plate 7.7, Figs. 5–8.

Pollen, monad, shape oblate, monosaccate, outline circular in polar view, equatorial diameter 62×77 µm under SEM, 64×85 µm under LM, leptoma; monosaccus coarsely folded; tectate, sculpture of leptoma verrucate (with granulate suprasculpture), proximal area rugulate (SEM).

*Occurrence*: 9–8 Ma sedimentary rock formation at Hrútagil.

**Sciadopityaceae**

***Sciadopitys* sp.** **P**

Plate 5.7, Figs. 1–3; Plate 6.11, Figs. 4–11; Plate 7.6, Figs. 7–9; Plate 9.5, Figs. 9–11; Plate 10.8, Figs. 9–11.

Pollen, monad, shape spheroidal, outline circular in polar view, equatorial diameter 18–35 μm under SEM, 26–38 μm under LM, leptoma, tectate, sculpture verrucate with microechinate suprasculpture and irregularly distributed perforations, central area of leptoma microechinate (SEM).

*Occurrence*: 12–4.0 sedimentary rock formations at Surtarbrandsgil (12 Ma), Tröllatunga (10 Ma), Hrútagil (9–8 Ma), Selárgil (5.5 Ma) and Tjörnes (Reká, 4.2–4.0 Ma).

## 3.7 Magnoliophyta

**Apiaceae**

For pollen morphology of modern members of Apiaceae see, for example, Punt (1984).

**Apiaceae gen. et spec. indet. 1** **P**

Plate 6.12, Figs. 1–4; Plate 10.9, Figs. 4–6.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis 17–18 μm, equatorial diameter ca 11 μm under SEM, 20–23 μm and 13–15 μm under LM, tricolporate, colpi ca 14 μm long (SEM), endopori lolongate rectangular, pollen wall ca 0.8 μm thick (LM), sexine thicker than nexine, pollen wall thickened in polar areas (ca 1.7 μm) and around endopori (ca 1.2 μm); sculpture microrugulate to rugulate, rugulae longer in polar area than in mesocolpium.

*Occurrence*: 10–4.0 Ma sedimentary rock formations at Tröllatunga (10 Ma) and Tjörnes (Egilsgjóta, Reká; 4.3–4.0 Ma).

**Apiaceae gen. et spec. indet. 2** **P**

Plate 6.12, Figs. 5–6.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis ca 16 μm, equatorial diameter ca 11 μm under SEM, ca 19 μm and ca 13 μm under LM, tricolporate, colpi ca 13 μm long (SEM), pollen wall 0.8–1.1 μm thick (LM), sexine thicker

than nexine, sexine slightly thicker along the colpi, surface sculpture microrugulate to rugulate, rugulae longer in the polar areas than in the mesocolpium (SEM).

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

**Apiaceae gen. et spec. indet. 3** **P**

Plate 6.12, Figs. 7–9.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis ca 18 µm, equatorial diameter ca 11 µm under SEM, ca 18 µm and ca 9 µm under LM, tricolporate, colpi ca 13 µm long (SEM), pollen wall 1–1.2 µm thick (LM), sexine thicker than nexine, sexine thickened around colpi in the mesocolpium, sculpture microrugulate to rugulate, rugulae longer in polar area than in the mesocolpium (SEM).

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

**Apiaceae gen. et spec. indet. 4** **P**

Plate 6.12, Figs. 10–13.

Pollen, monad, shape prolate, outline elliptic (bone shaped) in equatorial view, polar axis ca 28 µm, equatorial diameter ca 12 µm under SEM, ca 32 µm and ca 14 µm under LM, tricolporate, colpi ca 16 µm long (SEM), endopori lalongate elliptical, pollen wall 1.5–2.7 µm thick (LM), sexine thicker than nexine, sexine thickened around mesocolpium, sculpture microrugulate to rugulate, rugulae longer in polar area than in the mesocolpium (SEM).

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

**Apiaceae gen. et spec. indet. 5** **P**

Plate 7.8, Figs. 1–6.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis 15–17 µm, equatorial diameter 9–12 µm under SEM, 17–19 µm and ca 12 µm under LM, tricolporate, colpi 12–13 µm long (SEM), endopori lalongate, pollen wall 0.6–1.1 µm thick (LM), sexine thicker than nexine, sexine thickened around colpi, particularly in area around endopori; sculpture microrugulate to rugulate, rugulae oriented perpendicular to colpus (SEM).

*Occurrence*: 9–8 Ma sedimentary rock formation at Hrútagil.

**Apiaceae gen. et spec. indet. 6** **P**

Plate 9.6, Figs. 1–3; Plate 10.9, Figs. 1–3.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis 20–24 µm, equatorial diameter 13–16 µm under SEM, 23–24 µm and 17–18 µm

under LM, tricolporate, colpi 16–20 μm long (SEM), endopori lalongate, pollen wall 0.9–1.1 μm thick (LM), sexine thicker than nexine, sexine thickened along colpi in the mesocolpium, sculpture microrugulate to rugulate (SEM).

*Occurrence*: 5.5–4.0 Ma sedimentary rock formations at Selárgil (5.5 Ma) and Tjörnes (Egilsgjóta, Reká; 4.3–4.0 Ma).

**Apiaceae gen. et spec. indet. 7** **P**

Plate 9.6, Figs. 4–6.

Pollen, monad, shape prolate, outline elliptic (bone shaped) in equatorial view, polar axis ca 15 μm, equatorial diameter ca 7 μm under SEM, ca 17 μm and ca 10 μm under LM, tricolporate, endopori lalongate, pollen wall ca 0.8 μm thick (LM), sexine thicker than nexine, sculpture rugulate in polar area, microrugulate in mesocolpium (SEM).

*Occurrence*: 5.5 Ma sedimentary rock formation at Selárgil.

**Apiaceae gen. et spec. indet. 8** **P**

Plate 10.9, Figs. 7–9.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis ca 25 μm, equatorial diameter ca 11 μm under SEM, ca 30 μm and ca 15 μm under LM, tricolporate, colpi long, endopori lalongate, pollen wall 0.9–1.1 μm thick (LM), sexine thicker than nexine, sexine thickened in polar areas, sculpture microrugulate to rugulate, rugulae longer in polar areas than in mesocolpium, rugulae perpendicular to colpi in mesocolpium (SEM).

*Occurrence*: 4.3–3.8 Ma sedimentary rock formations at Tjörnes (Egilsgjóta, Reká, Skeifá).

**Apiaceae gen. et spec. indet. 9** **P**

Plate 10.9, Figs. 10–12.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis 36–42 μm, equatorial diameter 14–16 μm under SEM, 41–48 μm and 20–21 μm under LM, tricolporate, colpi 32–37 μm long (SEM), 39–41 μm (LM), endopori small rounded; pollen wall 1.7–2 μm thick (LM), sculpture rugulate (SEM).

*Occurrence*: 4.2–3.8 sedimentary rock formations at Tjörnes (Reká, Skeifá).

**Apiaceae gen. et spec. indet. 10** **P**

Plate 11.33, Figs. 4–6.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis ca 22 μm, equatorial diameter ca 11 μm under SEM, ca 22 μm and ca 11 μm under

LM, tricolporate, colpi ca 14 μm long (SEM), endopori lalongate, pollen wall ca 0.8 μm thick (LM), sexine thicker than nexine, sexine thickened in polar areas and central area of the mesocolpium, sculpture rugulate, rugulae longer in polar areas than in mesocolpium, rugulae often clustered in central (ridge) part of mesocolpium (SEM).

*Occurrence*: 0.8 Ma sedimentary rock formation at Svínafell.

### Aquifoliaceae

***Ilex* sp. 1** ('European Type') **P**

Plate 4.7, Figs. 1–6; Plate 5.8, Figs. 1–3; Plate 10.10, Figs. 1–3.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis 22–41 μm, equatorial diameter 19–31 μm under SEM, 27–49 μm and 23–40 μm under LM, tricolporate, colpi 13.1 μm long (SEM), sculpture clavate, clavae of different size, shorter along the apertures, clavae slightly to conspicuously striate in apical region, diameter of clavae in apical region up to 2 μm (SEM).

*Occurrence*: 15–3.8 Ma sedimentary rock formations at Botn (15 Ma), Surtarbrandsgil (12 Ma) and Tjörnes (Skeifá, 3.9–3.8).

*Remarks*: For pollen morphology of modern *Ilex* see, for example, Punt and Schmitz (1981).

***Ilex* sp. 2** **P**

Plate 7.8, Figs. 7–9.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis 30 μm, equatorial diameter 22 μm under SEM, 28 μm and 21 μm under LM, tricolporate, colpi 20 μm long (LM), sculpture clavate; clavae apically with low relief striation, diameter in apical region around 0.5 μm (SEM).

*Occurrence*: 9–8 Ma sedimentary rock formation at Hrútagil.

*Remarks*: This type differs from *Ilex* sp. 1 by its markedly smaller clavae.

### Araceae

***Lemna* sp.** **P**

Plate 5.13, Figs. 7–9.

Pollen, monad, shape spheroidal, outline circular in polar view, equatorial diameter 22–23 μm under SEM, 22–26 μm under LM, ulcerate, tectate; sculpture echinate, sparsely granulate; echinae oblong, psilate (SEM).

*Occurrence*: 12 Ma sedimentary rock formation at Surtarbrandsgil.

**Asteraceae**

***Artemisia* sp. 1** **P**

Plate 6.13, Figs. 1–4; Plate 11.4, Figs. 7–9.

Pollen, monad, shape spheroidal, outline circular in polar view, equatorial diameter 16–17 μm under SEM, polar axis ca 11 μm, equatorial diameter ca 20 μm under LM, tricolporate, eutectate, columellate, pollen wall 1.5–3 μm thick, with prominent exine, sexine thicker in the mesocolpium than around apertures (LM); sculpture echinate and granulate; echinae bluntly triangular in longitudinal section, space between echinae densely covered with granula.

*Occurrence*: 10–1.7 Ma sedimentary rock formations at Tröllatunga (10 Ma) and Bakkabrúnir (1.7 Ma).

***Artemisia* sp. 2** **P**

Plate 6.13, Figs. 5–10; Plate 9.6, Figs. 7–12; Plate 11.17, Figs. 10–12; Plate 11.33, Figs. 10–12.

Pollen, monad, shape spheroidal, outline trilobate in polar view, circular in equatorial view, polar diameter 15–17 μm, equatorial diameter 16–18 μm under SEM, 15–18 μm and 16–21 μm under LM, tricolporate, colpi 12–15 μm long (LM), eutectate, columellate, pollen wall 1.4–3.3 μm thick, with prominent exine, sexine thicker in the central mesocolpium than around apertures (LM); sculpture echinate to microechinate, echinae sharply triangular, regularly spaced, space between echinae densely covered with granulae and smaller microechinae (SEM).

*Occurrence*: 10–0.8 Ma sedimentary rock formations at Tröllatunga (10 Ma), Selárgil (5.5 Ma), Stöð (1.1 Ma) and Svínafell (0.8 Ma).

***Artemisia* sp. 3** **P**

Plate 11.33, Figs. 7–9.

Pollen, monad, shape prolate to spheroidal, outline elliptic in equatorial view, polar axis ca 17 μm, equatorial diameter ca 14 μm under SEM, polar axis ca 18 μm, equatorial diameter ca 14 μm under LM, tricolporate, colpus 9–10 μm under SEM, eutectate, columellate, pollen wall 1–1.2 μm thick, sculpture microechinate, microechinae widely spaced, area between echinae granulate (SEM).

*Occurrence*: 0.8 Ma sedimentary rock formation at Svínafell.

***Cirsium* sp.** **P**

Plate 10.10, Figs. 4–6.

Pollen, monad, shape oblate, outline trilobate, diameter 46–51 μm under SEM, 58–62 μm under LM, tricolporate, eutectate, columellate, sculpture echinate,

microreticulate, echinae bluntly triangular in profile, basal diameter of echinae 2.5–3.6 μm, height 2.8–3.2 μm, two to five echinae per 100 μm$^2$.

*Occurrence*: 4.2–4.0 sedimentary rock formation at Tjörnes (Reká).

**Asteraceae gen. et spec. indet. 1**
**[aff. *Lapsana communis*]** **P**

Plate 6.14, Figs. 1–3; Plate 7.8, Figs. 10–12; Plate 9.7, Figs. 1–3; Plate 10.10, Figs. 7–9; Plate 11.4, Figs. 10–12; Plate 11.18, Figs. 1–3.

Pollen, monad, shape spheroidal, outline subcircular, diameter 24–37 μm under SEM, 24–41 μm under LM, tricolporate, lophate, sculpture echinate, perforate, echinae triangular in profile, lophae are separated by lacunae; perforations becoming larger in basal parts of echinae, basal diameter of echinae 2.6–4 μm, height 3.6–5 μm.

*Occurrence*: 10–1.1 Ma sedimentary rock formations at Tröllatunga (10 Ma), Hrútagil (9–8 Ma), Selárgil (5.5 Ma), Tjörnes (Reká, 4.2–4.0 Ma), Bakkabrúnir (1.7 Ma) and Stöð (1.1).

**Asteraceae gen. et spec. indet. 2** **P**

Plate 6.14, Figs. 4–9; Plate 9.7, Figs. 4–6.

Pollen, monad, shape spheroidal, outline scircular, polar axis 26 μm, equatorial diameter 27–35 μm under SEM, diameter 29–38 μm under LM, tricolporate, eutectate, columellate, pollen wall 2–2.8 μm thick (LM), sculpture echinate, perforate, echinae pointed triangular in profile, evenly and widely distributed, occurring in rows, eight echinae per 100 μm$^2$, perforations very small between echinae, becoming conspicuously large around bases of echinae, basal diameter of echinae 2.9–3.7 μm, height 3.6–5.2 μm.

*Occurrence*: 10–5.5 Ma sedimentary rock formations at Tröllatunga (10 Ma) and Selárgil (5.5 Ma).

**Asteraceae gen. et spec. indet. 3** **P**

Plate 6.14, Figs. 10–12; Plate 11.34, Figs. 1–3.

Pollen, monad, shape spheroidal, outline trilobate in polar view, circular in equatorial view, equatorial diameter 24–26 μm under SEM, 22–29 μm under LM, tricolporate, eutectate, columellate, pollen wall ca 1.5 μm thick (LM), sculpture echinate, perforate, echinae pointed triangular in profile, evenly distributed, densely spaced, 12 echinae per 100 μm$^2$, small perforations confined to bases of echinae, basal diameter of echinae 1.4–2.6 μm, height 3.2–3.6 μm.

*Occurrence*: 10–0.8 Ma sedimentary rock formations at Tröllatunga (10 Ma), and Svínafell (0.8 Ma).

*Remarks*: This morphotaxon may comprise more than one biological species.

**Asteraceae gen. et spec. indet. 4 (*Ambrosia* sp.)** **P**

Plate 9.7, Figs. 7–9; Plate 11.18, Figs. 4–9 ; Plate 11.34, Figs. 4–6.

Pollen, monad, shape spheroidal, outline circular to lobate in polar view, diameter 10–21 μm under SEM, 14–26 μm under LM, tricolporate, eutectate, columellate, pollen wall ca 1.3–1.5 μm thick, 3.6 μm in mesocolpium (LM), sculpture echinate, perforate, echinae bluntly triangular in profile, evenly distributed, densely spaced, 17–42 echinae per 100 $\mu m^2$, small perforations confined to bases of echinae and tectum between echinae, basal diameter of echinae 1–1.3 μm, height 0.7–0.8 μm.

*Occurrence*: 5.5–0.8 Ma sedimentary rock formations at Selárgil (5.5 Ma), Stöð (1.1 Ma) and Svínafell (0.8 Ma).

**Asteraceae gen. et spec. indet. 5** **P**

Plate 10.11, Figs. 1–3.

Pollen, monad, shape spheroidal, outline lobate in polar view, circular in equatorial view, polar axis 30 μm, equatorial diameter 31 μm under SEM, equatorial diameter 35–37 μm under LM, tricolporate; eutectate, columellate, sculpture echinate, perforate; echinae pointed triangular in profile, evenly and widely distributed, four to five echinae per 100 $\mu m^2$, tectum between echinae and lower half of echinae with numerous perforations, basal diameter of echinae 4.1–4.6 μm, height 3–3.9 μm.

*Occurrence*: 4.3–4.2 Ma sedimentary rock formation at Tjörnes (Egilsgjóta).

**Asteraceae gen. et spec. indet. 6** **P**

Plate 10.11, Figs. 4–6.

Pollen, monad, shape spheroidal, outline circular in polar view, polar axis 25–30 μm, equatorial diameter 25–31 μm under SEM, polar axis 31–35 μm, equatorial diameter 31–36 μm under LM, tricolporate, colpi 18–19 μm long (LM), eutectate, columellate, sculpture echinate, perforate; echinae pointed triangular in profile, evenly distributed, 6–12 echinae per 100 $\mu m^2$, perforations smaller but distinct between echinae, becoming conspicuously large around bases of echinae, basal diameter of echinae 2.4–3 μm, height 3.9–4.8 μm.

*Occurrence*: 4.3–3.8 Ma sedimentary rock formations at Tjörnes (Egilsgjóta, Reká, Skeifá).

**Asteraceae gen. et spec. indet. 7** **P**

Plate 10.11, Figs. 7–9.

Pollen, monad, shape spheroidal to prolate, elliptic in equatorial view, polar axis 36 µm, equatorial diameter 29 µm under SEM, 42 and 36 µm under LM, tricolporate, colpi 18 µm long (SEM), 25 µm (LM); eutectate, columellate, sculpture echinate, perforate; echinae pointed triangular in profile, densely spaced, evenly distributed, four to five echinae per 100 µm$^2$, tectum between echinae and in basal parts of echinae perforate, basal diameter of echinae 4.2–4.4 µm, height 3–4.2 µm.

*Occurrence*: 4.2–4.0 Ma sedimentary rock formation at Tjörnes (Reká).

**Asteraceae gen. et spec. indet. 8** **P**

Plate 10.11, Figs. 10–12; Plate 11.18, Figs. 10–12; Plate 11.19, Figs. 1–3; Plate 11.34, Figs. 7–9.

Pollen, monad, shape spheroidal to prolate, outline lobate in polar view, circular to elliptic in equatorial view, polar axis 17–28 µm, equatorial diameter 13–27 µm under SEM, 20–27 µm and 18–25 µm under LM, tricolporate, colpi 11–13 µm long (SEM), 15–16 µm (LM); eutectate, columellate, sculpture echinate, perforate, echinae pointed or blunt triangular in profile, evenly distributed, four to eight echinae per 100 µm$^2$, tectum between echinae and lower half of echinae perforate, basal diameter of echinae 2.6–3.4 µm, height 1.3–2 µm (SEM).

*Occurrence*: 4.2–0.8 Ma sedimentary rock formations at Tjörnes (Reká, 4.2–4.0 Ma), Stöð (1.1 Ma) and Svínafell (0.8 Ma).

*Remarks:* This morphotaxon may comprise more than one biological species.

**Asteraceae gen. et spec. indet. 9** **P**

Plate 11.19, Figs. 4–9.

Pollen, monad, shape spheroidal, outline lobate in polar view, circular in equatorial view, polar axis 18 µm, equatorial diameter 16 µm under SEM, 23 µm and 20 µm under LM, tricolporate; colpi 12–13 µm long (SEM), 14–15 µm (LM); eutectate, columellate, sculpture echinate, perforate; echinae short triangular, densely spaced, ca 30 echinae per 100 µm$^2$, tectum between echinae and lower half of echinae with numerous perforations, basal diameter of echinae 4.1–4.6 µm, height 3–3.9 µm.

*Occurrence*: 1.1 Ma sedimentary rock formation at Stöð.

**Asteraceae gen. et spec. indet. 10** **P**

Plate 11.19, Figs. 10–12.

Pollen, monad, shape spheroidal, outline circular, diameter 26–27 μm under SEM, 31–32 μm under LM, tricolporate, lophate, sculpture echinate, densely perforate, echinae triangular in profile, lophae separated by lacunae; basal diameter of echinae 1.3–1.7 μm, height 1.3–1.6 μm.

*Occurrence*: 1.1 Ma sedimentary rock formation at Stöð.

*Remarks*: This pollen type is very similar to pollen of *Hieracium* and *Taraxacum*.

**Asteraceae gen. et spec. indet. 11** **P**

Plate 11.34, Figs. 10–12.

Pollen, monad, shape spheroidal, outline circular, diameter 25–27 μm under SEM, 26–28 μm under LM, tricolporate, lophate, sculpture echinate, densely perforate, echinae broad and rounded at base, abruptly constricted apically forming an oblong smooth spine, 6–18 echinae per 100 $\mu m^2$, echinae lophae separated by lacunae; basal diameter of echinae 2–2.7 μm, height 1.8–2.1 μm.

*Occurrence*: 0.8 Ma sedimentary rock formation at Svínafell.

**Asteraceae gen. et spec. indet. 12** **P**

Plate 11.35, Figs. 1–3.

Pollen, monad, shape spheroidal, outline lobate in polar view, circular in equatorial view, polar axis 24–25 μm, equatorial diameter 22–23 μm under SEM, 23–24 and 19–24 μm under LM, tricolporate, eutectate, columellate, sculpture echinate, densely perforate, perforations becoming slightly larger around bases of echinae, reaching one-third to halfway up echinae, echinae sharply triangular, seven to eight echinae per 100 $\mu m^2$, basal diameter of echinae 2.7–3.8 μm, height 2.1–2.3 μm.

*Occurrence*: 0.8 Ma sedimentary rock formation at Svínafell.

**Betulaceae**

***Alnus cecropiifolia* (Ettingshausen) Berger** **M**

Plate 5.9, Figs. 1–2, 4; Plate 6.15, Figs. 1–3; Plate 7.9, Figs. 1–3; Plate 8.5, Figs. 1–2.

1868 *Alnus kefersteinii* (Goepp.) Goepp. – Heer: p. 146, pl. 25, fig. 9b.
1886 *Alnus kefersteinii* (Goepp.) Goepp. – Windisch: p. 35, partim (foliage).
1966 *Alnus* sp. – Friedrich: p. 70, pl. 1, fig. 13, pl. 2, figs. 10, 11, text-fig. 18.

1972 *Alnus* sp. – Friedrich et al.: p. 8, pl. 1, fig. 4.
1983 *Alnus* sp. – Friedrich and Símonarson: fig. 6.
2005 *Alnus* sp. – Denk et al.: p. 378, figs. 50–51.
2005 *Alnus cecropiifolia* (Ettingshausen) Berger – Denk et al.: p. 380, figs. 56–58.
2008a *Alnus cecropiifolia* (Ettingshausen) Berger – Grímsson and Símonarson: fig. 18.

Leaves petiolate; petiole 7–16 mm long, lamina ovate to elliptic, 5–13 (–15) cm long and 3.5–9 cm wide, in some cases slightly triangularly lobed; base obtuse to slightly cordate, apex acute to acuminate, basalmost secondary veins almost perpendicular to primary vein, following secondaries forming angles between 30° and 45° to primary vein, margin double dentate/serrate with small obtuse to acute teeth, close to the base margin entire, teeth of two sizes, i.e. primary and secondary teeth present, secondary and abmedial veins running into primary teeth, secondary teeth served by veinlets branching off from tertiary veins or abmedial veins forming loops from which short veinlets supply teeth, up to 7 secondary teeth along the margin between two adjacent primary teeth, secondary venation craspedodromous, 8–12 pairs of secondary veins, opadial veins present, lowest secondary veins gently curved and subparallel to basal margin in many cases, sending off abmedial branches, higher up secondary veins relatively straight, tertiary veins oblique to perpendicular to secondary veins, simple or forked, about 4–11 tertiary veins per 1 cm secondary vein, course of quaternary veins orthogonal, areoles imperfect, veinlets branched twice or three times.

*Occurrence*: 12–6 Ma sedimentary formations at Seljá, Surtarbrandsgil (12 Ma), Húsavíkurkleif, Tröllatunga (10 Ma), Hrútagil (9–8 Ma), Hestabrekkur, Brekkuá and Þrimilsdalur (7–6 Ma).

*Remarks*: Many broad leaves of this type have been reported from Sarmatian and Pannonian/Pontian deposits of Poland, Hungary, Austria, Moravia, and Greece as *A. cecropiaefolia* (Ettingsh.) Berger. Knobloch (1969) mentioned the modern Mexican species *A. pringlei* Fernald as comparable to *A. cecropiifolia*, whereas later authors favoured affiliation with Eurasian alders, e.g. *A. glutinosa* subsp. *barbata* (C. A. Mey.) Yaltırık (Kvaček et al. 2002). Also, some North American *A. rhombifolia* Nutt. have leaves that resemble the fossil species in shape and show a dentate margin at the leaf base similar to the fossil.

### *Alnus gaudinii* (Heer) Knobloch and Z. Kvaček M

Plate 5.9, Figs. 7–10.

1983 *Juglans* sp. – Friedrich and Símonarson: fig. 10.
2005 cf. *Juglans* sp. – Denk et al.: p. 391, figs. 110–111.
2005 *Alnus* aff. *gaudinii* (Heer) Knobloch and Z. Kvaček – Denk et al.: p. 380, figs. 52–55.

Leaves petiolate; petiole rarely preserved, >4 mm long, lamina narrow ovate, 5–11 cm long, 3–4.5 cm wide, serrate, base cordate or rounded, apex acute, secondaries pinnate, more densely spaced in the lower part, steeper and less dense towards

the apex, in 8–11 pairs, curved towards the margin, semicraspedodromous, abmedial veins forming loops from which small veinlets supply teeth; teeth with long basal and short apical side. Carbonized tissue resistant to maceration so that only very thin adaxial cuticle fragments were obtained; cells quadrangular, straight-walled and faintly granular on outer periclinal walls.

*Occurrence*: 12 Ma sedimentary rock formation at Surtarbrandsgil.

*Remarks*: Similar leaves occur in several European Miocene localities, but secondary veins in these specimens are generally denser and the bases more acute. Knobloch and Kvaček (1976) first recognized the true nature of such leaves based on epidermal features. *Alnus nitida* (Spach.) Endl. from the Himalayas has been indicated by several authors as the living analogue. Foliage very similar to the Icelandic specimens is also found in *A. subcordata* C. A. Meyer and *A. japonica* Sieb. and Zucc.

### *Alnus* sp. aff. *A. viridis* (Chaix) DC. M

Plate 10.12, figs. 4–5; Plate 11.5, figs. 1–5; Plate 11.36, figs. 1–6; Plate 11.37, figs. 1–7.

1935 *Betula* sp. – Líndal: p.107, fig. 5.
1939 *Alnus* sp. – Líndal: p.269, pl. 18, figs. 2, 3.
1963 *Alnus viridis* – Thorarinsson: pl. 5, figs. 2, 3.
1978 *Alnaster viridis* (Spach.) Czerep. *fossilis* – Akhmetiev et al.: pl. 12, fig. 13.
1978 *Alnaster viridis* (Spach.) Czerep. *fossilis* – Akhmetiev et al.: pl. 15, figs. 3, 4, 8, 17, 18, 24.

Leaves, female strobili, winged seeds.

Leaves petiolate; petiole 5–19 mm long, lamina 3–10 cm long, 2.3–7.5 cm wide, length to width ratio 1–1.5, symmetrical, base asymmetrical in some cases, shape wide elliptic to suborbiculate, wide ovate to wide obovate, apex obtuse to acute, base acute, obtuse, rounded or cordate, margin serrate, teeth along whole margin or distal to the basalmost part, commonly groups of teeth forming lobes, teeth small and of approximately the same size or compound, basal and apical sides equally long or apical side shorter, primary teeth served by secondary veins and slightly larger than secondary teeth, secondary teeth served by branches of secondary veins, both primary and secondary teeth bearing minute subsidiary teeth in some cases, served by tertiary veins, 2–6 teeth between two adjacent primary teeth, primary vein straight, becoming zig-zag close to apex in some leaves, secondary venation craspedodromous, 7–11 pairs of secondary veins, mostly alternate, diverging from primary vein at angles of 35–45°(–60°), secondary veins straight or curving upwards, commonly branching, tertiary veins conspicuous, perpendicular to oblique to secondary veins, forked or rarely simple, convex, 3–7 tertiary veins per cm of secondary vein, areoles formed by quaternary and higher order veins, quadrangular to hexagonal. Female strobili 1–1.2 cm long, 8–11 mm wide, length to width ratio 1.1–1.3, suborbiculate.

Seeds winged, 3.1–4.1 mm long, 3.1–3.9 mm wide, length to width ratio 0.9–1.1, nutlet 2.6–3.3 mm long, 1.4–1.6 mm wide, length to width ratio 1.7–2.1, nutlets elliptic to narrow obovate, apex of nutlet acute with inconspicuous umbo with two short stigmas, stigmas 0.3–0.9 mm long, nutlet with marked longitudinal venation, wing 0.8–1.4 mm wide, widest in middle to upper part, longitudinal venation extending to wing.

*Occurrence*: 3.9–0.8 Ma sedimentary rock formations at Tjörnes (Skeifá, 3.9–3.8 Ma), Bakkabrúnir (1.7 Ma) and Svínafell (0.8 Ma).

*Remarks*: *Alnus* seeds with broad paper-like wings, relatively small strobili, and morphologically distinct leaves have clear affinities with the extant *Alnus viridis*. The modern species has an almost continuous circumpolar distribution including Greenland. In Europe, *A. viridis* is absent from Scandinavia and Iceland but common in the Alps (Meusel et al. 1965).

### *Alnus kefersteinii* (Goepp.) Unger M

Plate 5.9, Fig. 6; Plate 6.15, Figs. 4–6; Plate 7.9, Figs. 4–5; Plate 8.5, Figs. 3–6.

1865 *Sequoia sternbergii* (Goepp.) Heer – Heer: partim, text-fig. 161.
1868 *Alnus kefersteinii* (Goepp.) Unger – Heer: p. 146, pl. 25, figs. 4–9.
1886 *Alnus kefersteinii* (Goepp.) Unger – Windisch: p. 35, partim (infructescences).
1966 *Sequoia sternbergii* (Goepp.) Heer – Friedrich: p. 63, partim, text-fig. 14.
2005 *Alnus* cf. *kefersteinii* (Goepp.) Goepp. – Denk et al.: p. 380, figs. 59–62
2008a *Alnus* cf. *kefersteinii* (Goepp.) Goepp. – Grímsson and Símonarson: fig. 25.

Strobile-like infructescences, 1.3–2.4 cm long, 9–22 mm wide, medial and lateral bracteoles fused.

*Occurrence*: 12–6 Ma sedimentary rock formations at Surtarbrandsgil, Seljá (12 Ma), Húsavíkurkleif, Tröllatunga, Gautshamar (10 Ma), Hrútagil (9–8 Ma) and Brekkuá, Hestabrekkur and Þrimilsdalur (7–6 Ma).

*Remarks*: Infructescences of *Alnus* occur in most of the Miocene sedimentary formations of Iceland but cannot be linked to particular species because they are never attached to twigs bearing leaves.

### *Alnus* sp. 1 P

Plate 4.7, Figs. 7–12; Plate 5.9, Figs. 11–13; Plate 6.16, Figs. 1–6; Plate 7.9, Figs. 7–9; Plate 8.8, Figs. 1–3; Plate 9.10, Figs. 1–3; Plate 10.13, Figs. 1–3; Plate 11.6, Figs. 1–3.

Pollen, monad, shape oblate, outline pentangular rarely quadrangular in polar view, equatorial diameter 22–30 μm under SEM, and 23–34 μm under LM, pentaporate (tetraporate), pori 1.4–2.9 μm in diameter, pori annulate, arci connecting

apertures, arci 2.9–4.8 μm wide (SEM), tectate, columellate; pollen wall 0.7–1.5 μm thick (LM), sculpture rugulate to microrugulate, rugulae irregularly microechinate (SEM).

*Occurrence*: 15–1.7 Ma sedimentary rock formations at Botn (15 Ma), Surtarbrandsgil (12 Ma), Tröllatunga (10 Ma), Hrútagil (9–8 Ma), Hestabrekkur (7–6 Ma), Selárgil (5.5 Ma), Tjörnes (Egilsgjóta, Reká; 4.3–4.0 Ma) and Bakkabrúnir (1.7 Ma).

### *Alnus* sp. 2 P

Plate 6.16, Figs. 7–9.

Pollen, monad, shape oblate, outline pentangular in polar view, equatorial diameter 21–25 μm under SEM, and 25–28 μm under LM, pentaporate, porus 1.7–2.7 μm in diameter, pori annulate, arci connecting apertures, arci 2.5–2.8 μm wide (SEM), tectate, columellate; pollen wall 0.8–1.2 μm thick (LM), sculpture with polygonal raised areas separated by fossulae, polygonal areas irregularly microechinate (SEM).

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

### *Alnus* sp. 3 P

Plate 6.16, Figs. 10–15; Plate 10.13, Figs. 4–6; Plate 11.6, Figs. 4–6; Plate 11.6, Figs. 4–6; Plate 11.20, Figs. 1–6; Plate 11.35, Figs. 4–6.

Pollen, monad, shape oblate, outline pentangular rarely quadrangular in polar view, equatorial diameter 14–24 μm under SEM, and 16–26 μm under LM, pentaporate (tetraporate), pori 0.5–2.2 μm in diameter, pori annulate, arci connecting apertures, arci 1.5–2 μm wide (SEM), tectate, columellate; pollen wall 1.3–1.7 μm thick (LM), sculpture microrugulate to rugulate; rugulae irregularly microechinate (SEM).

*Occurrence*: 10–0.8 Ma sedimentary rock formations at Tröllatunga, Húsavíkurkleif (10 Ma), Tjörnes (Egilsgjóta, Skeifá; 4.3–4.0 Ma), Bakkabrúnir (1.7 Ma), Stöð (1.1 Ma) and Svínafell (0.8 Ma).

### *Betula cristata* Lindquist emend. Denk, Grímsson and Z. Kvaček M

Plate 7.10, Figs. 1–4; Plate 8.6, Figs. 1–9; Plate 8.7, Figs. 1–11; Plate 9.8, Fig. 2.

1859 *Betula forchhammeri* Heer – Heer: p. 318.
1868 *Betula macrophylla* (Goepp.) Heer – Heer: p. 146, pl. 25, figs. 11–19.
1868 *Betula prisca* Ettingsh. – Heer: p. 148, pl. 25, figs. 22–25.

1868 *Betula forchhammeri* Heer – Heer: p. 148, pl. 25, figs. 28, 29.
1947 *Betula cristata* Lindquist – Lindquist: p. 346, fig. 1: 1–5, fig. 2: 1–5.
1947 *Betula* sp. – Lindquist: p. 346, fig. 4: 3, 4.
1972 *Betula* sp. – Friedrich et al.: p. 8, pl. 1, fig. 3, pl. 3, fig. 1.
1978 *Betula macrophylla* (Goepp.) Heer – Akhmetiev et al.: pl. 9, figs. 3, 10, 12, pl. 10, figs. 1, 9, 11–13, pl. 11, fig. 1.
1978 *Betula subnivalis* Lindquist – Akhmetiev et al.: pl. 10, fig. 6, pl. 11, figs. 10, 14–16.
1978 *Betula* sp. 1 – Akhmetiev et al.: pl. 11, figs. 2–4.
1978 *Betula* ex sect. *Albae* – Akhmetiev et al.: pl. 11, figs. 9, 17.
2005 *Betula cristata* Lindquist emend. Denk, Grímsson and Z. Kvaček – Denk et al.: p. 382, figs. 63–70, 73–74.
2008a *Betula cristata* Lindquist emend. Denk, Grímsson and Z. Kvaček – Grímsson and Símonarson: fig. 24.

Leaves, fruit scales, seeds.

Leaves petiolate; petiole 5–21 mm long, lamina ovate to elliptic, 3–13 cm long, 2–8.5 cm wide, length to width ratio 1.2–1.6, serrate, base cordate, apex acute, secondary veins craspedodromous, 8–13 pairs, secondary veins, pectinal veins and their abmedial branches and external veins supplying teeth; teeth triangular with an attenuate glandular apex.

Scales of fruiting catkins, 6–7 mm long, 4–5 mm wide, with three elliptic and apically rounded lobes, central lobe longer than lateral lobes.

Seeds, winged; nutlet 2.1–4.4 mm long, 1.7–2.6 mm wide, suborbiculate, orbiculate, elliptic or obovate, length to with ratio 1.2–2, proximal part obtuse, apical pole bottleneck-shaped with remnants of two styles, styles 0.6–5 mm long, total length excluding stigmas 3–4.7 mm, width 2.3–5.8 mm.

*Occurrence*: 9–5.5 Ma sedimentary rock formations at Hrútagil (9–8 Ma) and Þrimilsdalur, Hestabrekkur, Brekkuá, Veiðilækur, Laxfoss, Stafholt (7–6 Ma) and Selárgil (5.5 Ma).

*Remarks*: Leaves of *B. cristata* are similar to *B. pseudolumnifera* Givulescu from the Upper Miocene of southern and western Europe. The latter has been compared with the modern Japanese *B. maximowicziana* Regel (Kvaček et al. 2002). However, teeth are slightly more attenuate and more densely spaced in *B. maximowicziana* than in *B. pseudolumnifera* and *B. cristata*. Dentition in *B. cristata* is quite similar to *B. pendula* Roth.

### *Betula islandica* Denk, Grímsson and Z. Kvaček M

Plate 5.10, Figs. 1–11.

1954 *Corylus* cf. *americana* fossilis Newberry – Áskelsson: p. 94, fig. 7.
1956 *Betula* sp. – Áskelsson: p. 44, figs. 1, a–b.
1966 *Corylus* sp. – Friedrich: p. 74, pl. 2, figs. 1, 2, 7, 8, text-fig. 20.

1966 *Betula* sp. – Friedrich: p. 74, pl. 2, figs. 5, 6.
1968 *Corylus* sp. – Friedrich: pl. 2, figs. 2a, b.
1978 *Betula* sp. – Akhmetiev et al.: pl. 1, fig. 8 (from Surtarbrandsgil).
1983 *Betula* sp. – Friedrich and Símonarson: figs. 6, 10.
2005 *Betula* sect. *Costatae* (Regel) Koehne sp. – Denk et al.: p. 385, fig. 80.
2007a *Betula* sp. – Grímsson et al.: p. 189, pl. 17, fig. 1.
2007b *Betula* sect. *Costatae* – Grímsson et al.: fig. 4, g.

Leaves and catkin scales.

Leaves petiolate; petiole 6–16 mm long; lamina broad ovate, serrate, 8–12.5 cm long, 5–7 cm wide, base cordate, apex acute to acuminate, secondary veins craspedodromous (9–)10–11 pairs, supplying (primary) teeth, abmedial branches of pectinal veins, external veins and veinlets that branch off at an angle of 90° from tertiary veins inserting (secondary) teeth, teeth of more or less equal size, broadly triangular, basal and apical sides convex, apex acuminate, glandular. Cuticles reflect only straight-walled polygonal cells of the adaxial epidermis and four to six-cellular bases of glandular trichomes scattered on veins, more common in smaller specimens.

Trilobed catkin scales of fruiting catkins 1.0–1.2 cm long and 7 mm wide, symmetrical, lobes long and narrow, linear, central lobe 7.7 mm long and 1–1.7 mm wide, 1.7–2.2 times longer than lateral lobes, which are 3.5–4.5 mm long, 1.2–1.4 mm wide and distinct from central lobe, narrow oblong, with bluntly acute apex; sinuses between lobes angular; proximal part or base of scale short and obtuse.

*Occurrence*: 13.5–10 Ma sedimentary rock formations at Ketilseyri (13.5 Ma), Surtarbrandsgil (12 Ma) and Húsavíkurkleif (10 Ma).

*Remarks*: This fossil species falls within the variability of the modern section *Costatae* (Regel) Koehne based on its large leaf size. Within the section *Costatae*, *B. islandica* shows similarities to the modern North American *B. alleghaniensis* Britt. (syn. *B. lutea* Michx.), and to the Eurasian species *B. utilis* D. Don and *B. ermanii* Cham.

The scales belong to section *Costatae* based on their long and narrow lobes. Mädler (1939) described very similar scales from the Pliocene of Germany as *B. longisquamosa*. Among living species, closest similarities are to the East Asian *B. delavayi* Franchet var. *delavayi*, and *B. chinensis* Maxim. var. *fargesii* Hu ex P. C. Li. *Betula* sect. *Costatae* displays an East Asian-North American disjunct distribution at present. The fossil record indicates that members of this section persisted in Europe at least until the Late Pliocene (Mädler 1939). Because of the presence of a single species based on leaves and on scales, both belonging to section *Costatae*, we suggest that these fossil types belong to a single biological species.

### *Betula* sp. A (section *Betulaster*) M

Plate 9.9, Figs. 1–3.

Fragment of upper two thirds of a leaf, lamina most likely ovate, apex acute, ca 12 pairs of secondary veins forming craspedodromous venation, margin dentate, teeth

of one size, 3–6 teeth between two adjacent primary teeth, teeth narrow triangular or reduced oblong glandular tips.

*Occurrence*: 5.5 Ma sedimentary rock formation at Selárgil.

*Remarks*: This leaf fragment most closely resembles leaves found in *Betula* section *Betulaster* (Spach) Regel. Modern species of this section are confined to East Asia. Recent phylogenetic studies based on molecular markers suggest that the sections traditionally recognized within *Betula* are most likely not monophyletic (e.g. Li et al. 2005).

### *Betula* sp. B M

Plate 10.12, Fig. 6.

Seed, winged; nutlet 2 mm long, 1.2 mm wide, length to width ratio 1.7, elliptic-ovate, entire seed 2.2 mm long and 2.7 mm wide.

*Occurrence*: 3.9–3.8 sedimentary rock formation at Skeifá.

### *Betula nana* L. x *pubescens* L. M

Plate 11.5, Figs. 6–7.

1978 *Betula* sp. ex sect. *Nanae* Rgl. – Akhmetiev et al.: pl. 15, figs. 20, 21.

Leaves, lamina suborbicular, 1.5 cm long, 1.6 cm wide, base rounded, apex bluntly acute, secondary venation craspedodromous, opadial vein present, basalmost pair of secondary veins with four abmedial branches, secondary veins, branches of secondary veins, and abmedial veins and their branches supplying teeth; teeth at base variable in size but becoming equal distally, 0–1 secondary teeth between two adjacent primary teeth.

*Occurrence*: 1.7 Ma sedimentary rock formation at Bakkabrúnir.

*Remarks*: This small fossil birch leaf may represent a hybrid between *B. nana* and *B. pubescens*. It is similar to *B. nana* in size but has a greater number of secondary veins and more teeth along the margin. It differs from *B. pubescens* by its much smaller size.

### *Betula* sp. P

Plate 4.8, Figs. 4–9; Plate 5.10, Figs. 12–14; Plate 6.17, Figs. 1–6; Plate 7.10, Figs. 5–7; Plate 8.8, Figs. 4–6; Plate 9.10, Figs. 4–11; Plate 10.13, Figs. 7–9; Plate 11.6, Figs. 7–9; 11.20, Figs. 7–12: 11.35, Figs. 7–9.

Pollen, monad, shape oblate, outline convex triangular in polar view, equatorial diameter 16–31 under SEM, and 20–32 μm under LM, angulaperturate, triporate, pori 1.4–2.5 μm in diameter (SEM), 2.2–2.7 μm (LM), pori annulate, vestibulum clearly

visible (LM), eutectate, columellate, pollen wall 0.7–1.5(−2.3) μm thick (LM); sculpture microrugulate to rugulate, rugulae covered with microechinae (SEM).

*Occurrence*: 15–0.8 Ma sedimentary rock formations at Botn (15 Ma), Surtarbrandsgil (12 Ma), Tröllatunga, Húsavíkurkleif (10 Ma), Hrútagil (9–8 Ma), Hestabrekkur (7–6 Ma), Selárgil (5.5 Ma), Tjörnes (Egilsgjóta, Reká; 4.3–4.0 Ma), Bakkabrúnir (1.7 Ma), Stöð (1.1 Ma) and Svínafell (0.8 Ma).

*Remarks*: Pollen of *Betula* is fairly homogeneous. Pollen referred here to *Betula* sp. may belong to different biological species.

### *Carpinus* sp. MT1 M

Plate 5.11, Figs. 1–2; Plate 7.11, Fig. 1.

? 1978 *Carpinus* sp. (?) – Akhmetiev et al.: pl. 8, fig. 6.

Leaves petiolate; petiole 1.5 cm long, lamina symmetrical with markedly asymmetrical basal part, lamina ovate, 12.0 cm long and 7.5 cm wide, length to width ratio 1.65, apex acute, base cordate, margin multi-serrate with small pointed teeth, apical and basal sides of teeth wide acuminate, sinuses between teeth angular, space between teeth commonly irregular, teeth in series, primary and secondary teeth of similar size and shape, tooth apex sharp, locally recurved, particularly in primary teeth, in other cases slender and sharp subsidiary teeth present, 3–4 secondary teeth between two adjacent primary teeth, secondary teeth served by branches of secondary veins or tertiary veins, subsidiary veins served by tertiary veins or their branches; primary vein slightly curved, of moderate thickness, secondary venation craspedodromous, 18 pairs of secondary veins, diverging from primary vein at angles of 77–37° above basal part of lamina, decreasing towards apex, secondary veins straight, 8–10 mm between two adjacent secondary veins in middle part of lamina, tertiary veins percurrent, simple or forked, perpendicular to secondary veins, 4–6 tertiary veins per 1 cm of secondary vein; quaternary veins orthogonal, quaternary and higher order veins forming areoles, areoles well developed, quadrangular to hexagonal, veinlets simple or branched.

*Occurrence*: 12–8 Ma sedimentary rock formations at Surtarbrandsgil (12 Ma) and Hrútagil (9–8 Ma).

*Remarks*: This leaf morphotype could belong to the same species as morphotype 2, described below. The same type of leaf dimorphism is common in living *Carpinus*.

### *Carpinus* sp. MT2 M

Plate 5.11, Figs. 3–4.

Leaves petiolate; petiole 5–5.5 mm long, lamina symmetrical, elliptic to narrow elliptic, 5.2–8.5 cm long and 2.3–3.2 cm wide, length to width ratio 2–2.6, apex

long acute, base cordate or round, in some cases slightly asymmetrical, margin multi-serrate with small pointed teeth, apical and basal sides of teeth straight or acuminate, sinuses between teeth narrow angular, teeth regularly spaced and compound, teeth in three series, primary teeth served by secondary veins, secondary teeth served by branches of secondary or tertiary veins, 0–3 (secondary) teeth between two adjacent secondary veins, apical side of teeth same or shorter than basal side; primary vein straight, of moderate thickness, secondary venation craspedodromous, 11–13 pairs of secondary veins, diverging from primary vein at angles of 51–27°, decreasing towards apex, secondary veins straight, 5–9.5 mm between two adjacent secondary veins.

*Occurrence*: 12 Ma sedimentary rock formation at Surtarbrandsgil.

### *Carpinus* sp. M

Plate 5.11, Fig. 5.

Winged fruit consisting of an oval bract and the attachment scar of the nut, bract only partly preserved, about 9 mm in diameter, oval, at least six veins originating from attachment scar forming loops close to distal margin of bract.

*Occurrence*: 12 Ma sedimentary rock formation at Seljá.

### *Carpinus* sp. 1 P

Plate 4.8, Figs. 10–12; Plate 5.11, Figs. 6–13.

Pollen, monad, shape oblate, outline convex triangular in polar view, equatorial diameter 24–32 μm under SEM, and 32–37 μm under LM, triporate pori 1.5–1.8 μm in diameter (SEM), pori annulate, without a vestibulum (LM), eutectate, columellate, pollen wall 1.1–1.3 μm thick (LM); sculpture rugulate to microrugulate, rugulae variable in length, rugulae irregularly microechinate (SEM).

*Occurrence*: 15–12 Ma sedimentary rock formations at Botn (15 Ma) and Surtarbrandsgil (12 Ma).

### *Carpinus* sp. 2 P

Plate 6.17, Figs. 7–12.

Pollen, monad, shape oblate, outline elliptic in polar view, equatorial diameter 23–34 μm under SEM, and 31–41 μm under LM, tetraporate to hexaporatetriporate, pori 1.2–3.1 μm in diameter (SEM), pori annulate, without a vestibulum (LM), eutectate, columellate, pollen wall ca 1.2 μm thick (LM); sculpture rugulate to microrugulate, rugulae irregularly microechinate (SEM).

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

***Corylus* sp.** **M**

Plate 5.12, Figs. 1–3.

2005 *Corylus* sp. – Denk et al.: p. 385, figs. 81–86.

Leaves, petiole not preserved, lamina broad ovate to elliptic, serrate, 10–14 cm long, 6 to >8 cm wide, base round to slightly cordate, apex acute, secondary veins craspedodromous, 8–11 pairs, with numerous abmedial branches, close to the margin abmedial veins are connected by a tertiary vein running parallel to the margin, from this vein short veinlets run into teeth; teeth triangular when inserted by secondary veins and almost round when inserted by higher-order veinlets, tooth apex acute to bluntly acute.

*Occurrence*: 12 Ma sedimentary rock formation at Surtarbrandsgil and possibly Seljá.

*Remarks*: Foliage unambiguously ascribable to *Corylus* appears to be rare in the fossil record of the Northern Hemisphere (cf. Mai 1995). Leaves named *Corylus avellana* L. *fossilis* from the Pliocene of Germany (Knobloch 1998) belong with certainty to the genus and are very similar to the fossils from Iceland. Among modern species, the western Eurasian *C. avellana* L. and *C. colchica* Albov., and the East Asian *C. chinensis* Franch. have similar foliage.

***Corylus* sp.** **P**

Plate 6.17, Figs. 13–15.

Pollen, monad, shape oblate, outline convex triangular in polar view, equatorial diameter 20–22 under SEM, and 25–26 μm under LM, angulaperturate, triporate, pori ca 0.8 μm in diameter (SEM), tectate, columellate, pollen wall 1.2–1.5 μm thick (LM); sculpture rugulate to microrugulate, rugulae irregularly microechinate (SEM).

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

*Remarks*: See Blackmore et al. (2003) for the pollen morphology of extant *Corylus* and other Betulaceae.

**Calycanthaceae**

**aff. Calycanthaceae sp.** **M**

Plate 5.24, Figs. 1–3.

2005 *Dicotylophyllum* sp. 1 – Denk et al.: p. 404, figs. 200–202.

Lamina elliptic, narrow elliptic, or ovate, 5–11.3 cm long, 2.8–7 cm wide, length to width ratio 1.9–2.5, petiole not preserved in most cases, 9.5 mm in one specimen, base acute to round, apex acute to acuminate, primary vein straight, 9–12 secondary veins, 5–19 mm between adjacent secondary veins, secondary veins diverging from primary vein at 41–63°, secondary venation brochidodromous, followed by higher-

order loops, course of venation very well preserved, leaf margin entire, rarely crenulate.

*Occurrence*: 12 Ma sedimentary rock formation at Surtarbrandsgil.

**aff. Calycanthaceae sp.** **P**

Plate 5.27, Figs. 4–12; Plate 6.18, Figs. 1–12; Plate 7.11, Figs. 3–5; Plate 8.8, Figs. 7–9; Plate 9.11, Figs. 1–3; Plate 10.13, Figs. 10–12.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis 18–32 μm, equatorial diameter 11–24 μm under SEM, 20–38 μm and 122–28 μm under LM, di-tricolpate, colpi 19.4–26 μm long (SEM), 27.5 μm (LM); tectate, columellate, pollen wall 0.6–1.7 μm thick (LM); sculpture perforate with ridges and furrows radiating from perforation pits (star-like), colpus rim with small perpendicular grooves.

*Occurrence*: 12–4.0 Ma sedimentary rock formations at Surtarbrandsgil (12 Ma), Tröllatunga, Húsavíkurkleif (10 Ma), Hrútagil (9–8 Ma), Hestabrekkur (7–6 Ma), Selárgil (5.5 Ma) and Tjörnes (Reká, 4.2–4.0 Ma).

*Remarks*: Pollen of the extant genus *Chimonanthus* is very similar to the fossil pollen. *Chimonanthus* has dicolpate to tricolpate pollen and a sculpturing as in the fossil forms. However, no colpus rim has been observed in *Chimonanthus*. *Calycanthus* has a smooth perforate tectum.

**Campanulaceae**

***Campanula* sp.** **P**

Plate 10.14, Figs. 1–3.

Pollen, monad, shape oblate to spheroidal, outline circular, diameter 24–25.3 μm under SEM, and 30–34 μm under LM, tetraporate, pores 2.3–2.8 μm in diameter; eutectate, columellate, pollen wall 1 μm thick (LM); sculpture rugulate, foveolate, echinate, echinae triangular in outline, bases of echinae formed by fusion of rugulae elongations (SEM).

*Occurrence*: 4.2–4.0 Ma sedimentary rock formation at Tjörnes (Reká).

**Caprifoliaceae**

***Lonicera* sp.** **M**

Plate 5.8, Figs. 4–5.

1978 *Lonicera* sp. – Akhmetiev et al.: pl. 8, fig. 1.
2005 *Dicotylophyllum* sp. 2 (‘*Lonicera*’) – Denk et al.: p. 404, figs. 203–206.

2007a *Dicotylophyllum* sp. 1 (‘*Lonicera*’) – Grímsson et al.: p. 207, pl. 9, 5–6.
2007b *Dicotylophyllum* sp. 1 (‘*Lonicera*’) – Grímsson et al.: fig. 7, b.

Leaves petiolate; petiole >3 mm long, lamina elliptic, entire, (2.1–)5.5–11.1 cm long, (1–)1.7–3.2 cm wide, length to width ratio 2–2.4, base acute or round, apex acute to attenuate, eight to ten pairs of secondary veins irregularly spaced, 0–2 intersecondary veins, secondary veins diverging from primary vein at angles of 43–25°, secondary venation incomplete brochidodromous, main loops followed by additional loops, tertiary venation pattern orthogonal reticulate, quaternary venation pattern orthogonal.

*Occurrence*: 15–12 Ma sedimentary rock formations at Selárdalur (15 Ma) and Surtarbrandsgil (12 Ma).

### *Lonicera* sp. 1 P

Plate 5.8, Figs. 6–8; Plate 6.19, Figs. 1–6.

Pollen, monad, shape oblate to spheroidal, outline convex triangular to circular in polar view, equatorial diameter 40–48 under SEM, and 46–65 μm under LM, tricolporate, eutectate, columellate, pollen wall 1.2–1.3 μm thick (LM); sculpture rugulate-fossulate, covered with equally distributed echinae; echinae 1–1.3 μm long, conical, interspersed microechinae (SEM).

*Occurrence*: 12–10 Ma sedimentary rock formations at Surtarbrandsgil (12 Ma), and Tröllatunga (10 Ma).

### *Lonicera* sp. 2 P

Plate 6.19, Figs. 7, 8, 12.

Pollen, monad, shape oblate to spheroidal, outline circular in equatorial view, equatorial diameter 68–74 under SEM, and 82–92 μm under LM, tricolporate, eutectate, columellate, pollen wall ca 2.2 μm thick (LM); sculpture rugulate, rugulae thin and oblong, fused in some cases, with equally distributed echinae, echinae 2.2–2.7 μm long, conical (SEM).

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

### *Lonicera* sp. 3 P

Plate 6.19, Figs. 9–11.

Pollen, monad, shape oblate to spheroidal, outline triangular in polar view, equatorial diameter 66–73 under SEM, and 82–95 μm under LM, tricolporate, eutectate, columellate, pollen wall ca 2.2 μm thick (LM); sculpture perforate, foveolate, echinate, echinae varying in size (SEM).

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

***Viburnum* sp.** **P**

Plate 4.9, Figs. 1–9; Plate 5.8, Figs. 9.14.

Pollen, monad, shape prolate, outline in equatorial view elliptic, polar axis 23–29 μm, equatorial diameter 16–23 μm under SEM, 28–37 μm and 20–31 μm under LM, tricolporate, colpi ca 25 μm long (SEM), semitectate, sculpture clavate, clavae forming incomplete reticulum, blunt microechinae on and between clavae (SEM).

*Occurrence*: 15–12 Ma sedimentary rock formations at Botn (15 Ma) and Surtarbrandsgil (12 Ma).

**Caryophyllaceae**

For pollen morphology of modern Caryophyllaceae, see Punt and Hoen (1995).

**Caryophyllaceae gen. et spec. indet. 1** **P**

Plate 6.20, Figs. 1–9; Plate 10.14, Figs. 4–6.

Pollen, monad, shape spheroidal, outline weakly polygonal, 13–21 μm in diameter under SEM and 16–22 μm under LM, pantoporate, (15–) 18–20 pori; tectate, columellate, pollen wall 1.2–1.9 μm thick, with relatively thick sexine (LM); sculpture microechinate, densely perforate, microechinae conical, 21–35 per 50 $\mu m^2$ in non-apertural regions, apertures sunken, aperture membrane densely covered with blunt microechinae of different size, 350–700 nm in cross-section (SEM).

*Occurrence*: 10–4.2 Ma sedimentary rock formations at Tröllatunga, Húsavíkurkleif (10 Ma) and Tjörnes (Egilsgjóta, 4.3–4.2).

**Caryophyllaceae gen. et spec. indet. 2** **P**

Plate 6.21, Figs. 1–4.

Pollen, monad, shape spheroidal, outline polygonal, diameter 16–17 μm under SEM and 20–22 μm under LM, pantoporate, 18–20 pori; tectate, columellate, pollen wall ca 1.6 μm thick, with a relatively thick sexine (LM); sculpture microechinate, perforate; microechinae 22 per 50 $\mu m^2$ non-apertural region, apertures sunken, aperture membrane densely covered with microechinae of different size, ca 500 nm in cross-section at the base (SEM).

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

**Caryophyllaceae gen. et spec. indet. 3** **P**

Plate 6.20, Figs. 10–12; Plate 8.8, Figs. 10–12.

Pollen, monad, shape spheroidal, outline circular to polygonal, diameter 31–39 μm under SEM and 33–50 μm under LM, pantoporate, 18–27 pores; apertures sunken,

pore diameter 2.2–4.3 μm, pori widely spaced, pollen tectate, columellate, pollen wall ca 0.9–1.5 μm thick, sculpture with numerous densely spaced perforations and microechinae that are confined to ridges between pores.

*Occurrence*: 10–6 Ma sedimentary rock formations at Tröllatunga (10 Ma) and Hestabrekkur (7–6 Ma).

**Caryophyllaceae gen. et spec. indet. 4 (*Stellaria*)** **P**

Plate 9.11, Figs. 4–6 ; Plate 10.14, Figs. 7–9.

Pollen, monad, shape spheroidal, outline weakly circular to weakly polygonal, 18–28 μm in diameter under SEM and 23–34 μm under LM, pantoporate, 15–18 pori; tectate, columellate, pollen wall ca 1.2 μm thick; sculpture microechinate, perforate; microechinae evenly distributed, 33–40 per 50 $\mu m^2$, perforations usually large and oblong, apertures sunken, aperture membrane with multipointed microechinae (SEM).

*Occurrence*: 5.5–3.8 Ma sedimentary rock formations at Selárgil (5.5 Ma), Tjörnes (Egilsgjóta, Reká, Skeifá; 4.3–3.8 Ma).

*Remarks*: This distinct pollen type is very similar to pollen of *Stellaria* (e.g. Punt and Hoen 1995, plates 130, 131).

**Caryophyllaceae gen. et spec. indet. 5** **P**

Plate 10.14, Figs. 10–12; Plate 11.6, Figs. 10–12.

Pollen, monad, shape spheroidal, outline circular, 25–29 μm in diameter under SEM and 32–36 μm under LM, pantoporate, 27–30 pori; tectate, columellate, pollen wall 1.3–1.5 μm thick; sculpture microechinate, perforate; microechinae evenly distributed, ca 50 per 50 $\mu m^2$, apertures sunken, aperture membrane with multipointed microechinae (SEM).

*Occurrence*: 4.3–1.7 Ma sedimentary rock formations at Tjörnes (Egilsgjóta; 4.3–4.2). and Bakkabrúnir (1.7 Ma).

**Caryophyllaceae gen. et spec. indet. 6** **P**

Plate 11.8, Figs. 1–3

Pollen, monad, shape spheroidal, outline circular, 16–23 μm in diameter under SEM and 20–27 μm under LM, pantoporate, 30–33 pori, pori small, 0.7–0.9 μm in diameter; tectate, columellate, pollen wall ca 1.4 μm thick, sexine thicker than nexine; sculpture microechinate, perforate, microechinae evenly distributed, ca 55 per 50 $\mu m^2$, apertures sunken, aperture membrane microechinate (SEM).

*Occurrence*: 1.7 Ma sedimentary rock formations at Bakkabrúnir.

**Caryophyllaceae gen. et spec. indet. 7** **P**

Plate 11.8, Figs. 4–6.

Pollen, monad, shape spheroidal, outline circular to weakly polygonal, 18–21 μm in diameter under SEM and 21–23 μm under LM, pantoporate, 12–15 pori, diameter of pori 1.8–2.5 μm, tectate, columellate, pollen wall 1.3 μm thick; sexine thicker than nexine, sculpture microechinate, perforate, microechinae densely spaced, apertures sunken, aperture membrane microechinate (SEM).

*Occurrence*: 1.7 Ma sedimentary rock formation at Bakkabrúnir.

**Caryophyllaceae gen. et spec. indet. 8** **P**

Plate 11.21, Figs. 1–3, 7–12.

Pollen, monad, shape spheroidal, outline circular, 15–35 μm in diameter under SEM and 22–42 μm under LM, pantoporate, 33–56 pori; diameter of pori 1.1–1.4 μm; tectate, columellate, pollen wall 1.5–1.7 μm thick, sexine much thicker than nexine; sculpture microechinate, perforate, microechinae evenly distributed; apertures sunken, with an operculum composed of multipointed microechinae (SEM).

*Occurrence*: 1.1 Ma sedimentary rock formation at Stöð.

**Caryophyllaceae gen. et spec. indet. 9** **P**

Plate 11.21, Figs. 4–6.

Pollen, monad, shape spheroidal, outline circular, 28–37 μm in diameter under SEM and 33–43 μm under LM, pantoporate, 18–21 pori, diameter of pori 2.4–4.3 μm; tectate, columellate, pollen wall ca 1.2 μm thick, sexine thicker than nexine; sculpture microechinate, perforate; microechinae evenly distributed, perforations large, especially around apertures, apertures sunken, with an operculum composed of microechinae (SEM).

*Occurrence*: 1.1 Ma sedimentary rock formation at Stöð.

**Ceratophyllaceae**

***Ceratophyllum* sp.** **M**

Plate 8.7, Figs. 12–15.

Endocarps, shortly pedicellate, endocarp (spines not measured) 3.8–5.4 mm long and 2.5–4 mm wide, with 10–14 prominent spines borne on basal and apical parts

of endocarp, spines 3–5.5 mm long; in one specimen perianth preserved, basal protuberances present, apically remnants of persistent style preserved.

*Occurrence*: 7–6 Ma sedimentary rock formation at Brekkuá and Hestabrekkur.

*Remarks*: Resembles the modern cosmopolitan *Ceratophyllum submersum* subsp. *muricatum* (Cham.) Wilmot-Dear (1985).

## Cercidiphyllaceae

### *Cercidiphyllum* sp. M

Plate 4.10, Figs. 5–6.

2007a *Cercidiphyllum* sp. – Grímsson et al.: p. 191, pl. 5, figs. 1–10.
2007b *Cercidiphyllum* sp. – Grímsson et al.: figs. 4, h–n.

Leaves petiolate; up to 2.9 cm long, lamina (3.0–)4.5–9.0 cm long and (3.0–) 4.0–8.4 cm wide, length to width ratio 1–1.2, widest below middle, symmetrical or slightly asymmetrical, broad ovate to suborbiculate, base cordate, margin entire close to base, crenate above; teeth large when present, 1–2 per cm margin, sinuses deeply rounded, gland at apical side of tooth, just above superadjacent sinus, slightly emergent; venation actinoacrodromous, five to seven primary veins, central primary vein straight in proximal part, flanked by two or three pairs of lateral primary veins, first strong secondary vein originating at an angle of 60° from central primary vein above the widest portion of lamina, lateral primary veins originating from a single point at leaf base; inner primary veins straight until point of origin of first outer secondary vein, then curving up towards central vein, forming angles of 30–40° with central vein, basal outer secondary veins arising at angles of 50–70°; outer primary veins curved, forming angles of 75–80° with central vein (55–60° when three pairs of lateral primary veins present), forming loops and joining outer secondary veins from the inner primary veins, secondaries forming primary loops, primary loops followed by secondary loops, from which small veins run into teeth; in the case of three pairs of lateral primary veins the outer primary veins arise from the central vein at angles of 94–125°; secondary venation semicraspedodromous or brochidodromous; 3–5 tertiary veins per cm of primary or secondary vein, marginal ultimate venation looped.

*Occurrence*: 15 Ma sedimentary rock formation at Selárdalur.

*Remarks*: The type of venation, the crenulated glandular margin, and the position of the glands suggest that these leaves belong to *Cercidiphyllum*. Similar leaves are abundant in Palaeogene floras from high latitude regions in the Northern Hemisphere (Far East, Budantsev 1997; Axel-Heiberg Island, Basinger 1991; Spitsbergen, Schloemer-Jäger 1958; Kvaček et al. 1994; Isle of Mull, Boulter and Kvaček 1989) and have been ascribed both to the extant genus *Cercidiphyllum* and to various extinct morphogenera (cf. list of synonyms in Schloemer-Jäger 1958). In

the late Cainozoic, such leaves are commonly referred to *Cercidiphyllum crenatum* (Unger) Brown (North America, La Motte 1936; Europe, Ferguson 1971; Kovar-Eder et al. 2004; Central Asia, Shilin 1974; Japan, Ozaki 1991). These leaves show considerable morphological plasticity regarding size, shape, and particularly tooth architecture, as found in the two living species *C. japonicum* Sieb. and Zucc. and *C. magnificum* (Nakai) Nakai.

***Cercidiphyllum* sp.** **P**

Plate 4.10, Figs. 1–4.

Pollen, monad, shape oblate, outline triangular in polar view, equatorial diameter 26–27 μm under SEM, 29–31 μm under LM, tricolporate, colpi wide; sculpture microreticulate, muri microechinate, aperture membrane densely covered by non-continuous microechinate sexine elements (SEM).

*Occurrence*: 15 Ma sedimentary rock formation at Botn.

*Remarks*: Extant pollen of *Cercidiphyllum* has been described by Praglowski (1974).

**Chenopodiaceae**

***Chenopodium* sp.** **P**

Plate 6.22, Figs. 1–3.

Pollen, monad, shape spheroidal, outline circular, diameter ca 23 μm under SEM, 26–28 μm under LM, pantoporate, 58–63 pori, 1.1–1.4 in diameter, pollen wall 1.4–1.8 μm thick (LM); sculpture microechinate, perforate, microechinae evenly distributed, widely spaced, ca 32 echinae per 50 $\mu m^2$, 0–3 echinae per 1 $\mu m^2$, aperture membrane (operculum) covered with microechinae.

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

**Chenopodiaceae gen. et spec. indet. 1**

Plate 6.22, Figs. 4–6.

Pollen, monad, shape spheroidal, outline circular, diameter 18–19 μm under SEM, 19–20 μm under LM, pantoporate, 63–69 pori, ca 0.9 μm in diameter, sunken; pollen wall 1.5–1.8 μm thick (LM); sculpture microechinate, perforate, microechinae irregularly distributed, 2–6 echinae per $\mu m^2$, aperture membrane (operculum) covered with microechinae.

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

**Chenopodiaceae gen. et spec. indet. 2** **P**

Plate 6.22, Figs. 7–9.

Pollen, monad, shape spheroidal, outline circular, diameter 21–22 μm under SEM, 21–22 μm under LM, pantoporate, 39–42 pori, ca 1.6 μm in diameter, slightly sunken, pollen wall 1.2–1.3 μm thick (LM); sculpture microechinate, perforate, microechinae densely spaced, 5–7 echinae per 1 $\mu m^2$, aperture membrane (operculum) covered with microechinae (SEM).

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

**Chenopodiaceae gen. et spec. indet. 3** **P**

Plate 10.15, Figs. 1–3; Plate 11.35, Figs. 10–12.

Pollen, monad, shape spheroidal, outline circular, diameter 17–18 μm under SEM, 17–18 μm under LM, pantoporate, 72–75 pori, 0.8–1.3 in diameter, sunken; sculpture microechinate, perforate, microechinae evenly distributed, aperture membrane (operculum) covered with microechinae.

*Occurrence*: 4.2–0.8 Ma sedimentary rock formations at Tjörnes (Reká, 4.2–4.0 Ma) and Svínafell (0.8 Ma).

**Cornaceae**

***Cornus* sp.** **M**

Plate 7.11, Fig. 2.

Leaf, preserved part of petiole 7 mm, lamina elliptic, estimated ca 12 cm long, 6.7 cm wide, base slightly decurrent, margin entire, secondary venation camptodromous-eucamptodromous, secondary veins characteristically curved upwards and converging close to apex, seven pairs of secondary veins, diverging at 51–15° from primary vein, angle markedly decreasing towards apex, tertiary veins percurrent, perpendicular to primary vein.

*Occurrence*: 9–8 Ma sedimentary formation at Hrútagil.

**Cyperaceae**

***Kobresia* sp.** **P**

Plate 10.15, Figs. 4–6; Plate 11.8, Figs. 7–9.

Pollen, pseudomonad, shape prolate, outline elliptic, polar axis 31.2–37 μm, equatorial diameter 24.2–28 μm under SEM, 36.7–44.2 μm and 30–30.8 μm under LM, pentaporoidate, one distal ulcus and four lateral apertural zones (poroids); sculpture fossulate, perforate, microechinate; aperture membrane composed of sexine elements.

*Occurrence*: 4.2–1.7 Ma sedimentary rock formations at Tjörnes (Reká, 4.2–4.0 Ma) and Bakkabrúnir (1.7 Ma).

*Remarks*: The sculpturing seen in the fossil grains is identical with the one found in the living *Kobresia myosuroides* (see Nagels et al. 2009, Fig. 3b).

### *Carex* sp. M

Plate 10.16, Figs. 5–6.

Axis with leaves and inflorescences in attachment, isolated infructescences, rhizomes attached to leafy axes. Rhizomes 2.0 to >3.0 cm long, 2.3–2.8 mm in diameter, slightly constricted at nodes, leaf scales arising from each node.
Aerial shoots >2 cm long, 1.3–2 mm in diameter, only terminal parts preserved, bluntly trigonous in cross-section, axis bearing leaves and inflorescence; leaves alternate, forming sheath around stem, leaves >3.0 cm long, 2.6–4.5 mm wide, with 10–20 parallel veins across width of leaf, leaves with midrib channel, keeled to plicate in cross-section, margin entire; inflorescence consisting of a single female spike (no male flowers present), spikes >2.0 cm long, 2–4 mm wide, cylindrical, subsessile, composed of utricles and glumes; glumes on abaxial side of utricles, 2.2–3.0 mm long, 0.9–1.1 mm wide, elliptic to narrow elliptic, apex acute; utricles 2.2–3.0 mm long including beak, 1.1–1.4 mm wide, widest in middle to upper part (below beak), elliptic to obovate in form, beak 6–7 mm long, utricles keeled on abaxial side. Isolated infructescence axes with mature fruits, beaks of mature fruits ca 11 mm long.

*Occurrence*: 3.9–3.8 sedimentary rock formation at Tjörnes (Skeifá).

### Cyperaceae gen. et spec. indet. A M

Plate 5.16, Figs. 7–8; Plate 6.23, Fig. 1.

1978 *Arundo* sp. – Akhmetiev et al.: pl. 2, fig. 12, pl. 7, fig. 5.

Fragments of leaves showing a distinct midrib and parallelodromous venation as found in many members of Cyperaceae.

*Occurrence*: 12–10 Ma sedimentary rock formation at Seljá and Surtarbrandsgil (12 Ma), Húsavíkurkleif and Tröllatunga (10 Ma).

### Cyperaceae gen. et spec. indet. B M

Plate 8.9, Figs. 1–5.

Achenes, elliptic in outline, 3–5 mm long, summit with style base, style base up to 0.5 mm high, notched, constricted or truncated slightly protruding proximal end corresponding to point of attachment.

*Occurrence*: 7–6 Ma sedimentary rock formation at Hestabrekkur.

**Cyperaceae gen. et spec. indet. C** **M**

Plate 11.39, Fig. 1.

Fragments of leaves, preserved parts of lamina up to 7.5 cm long, up to 7.1 mm wide, venation parallelodromous, leaves narrowing towards apex, with a midrib channel, folded or plicate in transverse section.

*Occurrence*: 0.8 Ma sedimentary formation at Svínafell.

**Ericaceae**

***Arctostaphylos* sp.** **M**

Plate 6.23, Figs. 2–3.

? 1868 *Phyllites vaccinioides* Heer – Heer: p. 154, pl. 27, fig. 13.
2005 cf. '*Arctostaphylos'* sp. – Denk et al.: p. 388, figs. 95–96.

Lamina elliptic, dentate, no petiole preserved, ca 1.4 cm long, 8 mm wide, base probably acute, apex rounded, slightly emarginate, secondary veins brochidodromous, about seven pairs, first-order loops followed by second-order loops from which small veins supply the teeth; teeth small, appressed, glandular.

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

*Remarks*: These leaves closely resemble deciduous species of *Arctostaphylos* and *Vaccinium*.

***Empetrum nigrum* L.** **M**

Plate 11.22, Fig. 1.

Leafy axis, >2 cm long, leaves densely spaced, spirally arranged, with a very short petiole, 1.5–2.2 mm long, 0.5–0.8 mm wide, length to width ratio 1.9–4.4, edges of lamina enrolled, on one side a deep furrow, lamina oblong, elliptic to narrow elliptic, base acute, apex bluntly acute, margin entire.

*Occurrence*: 1.1 Ma sedimentary rock formation at Stöð.

*Remarks*: The fossil leaves show morphological similarities to those of *Loiseleuria* and *Phyllodoce*. They differ from *Loiseleuria* by their spiral arrangement of the leaves, and from *Phyllodoce* by being tube–like.

***Rhododendron* aff. *ponticum* L.** **M**

Plate 6. 24, Figs. 1–3; Plate 8.9, Figs. 6–8; Plate 10.16, Figs. 1–4.

1978 (?) *Rhododendron* sp. – Akhmetiev et al.: pl. 10, fig. 14.
1978 *Phyllites* cf. *Rhododendron* sp. – Akhmetiev et al.: pl. 13, figs. 7–8.

2005 *Rhododendron* aff. *ponticum* L. – Denk et al.: p. 386, figs. 87–90.
2008a *Rhododendron* sp. – Grímsson and Símonarson: fig. 17.

Leaves petiolate; petiole 5–22 mm long, lamina elliptic to obovate, entire, 4.8–15 cm long, 1.3–4.6 cm wide, base acute to rounded, in some cases slightly decurrent, apex bluntly acute with a pointed tip, secondary veins eucamptodromous to brochidodromous, 8–12 pairs, locally intersecondary veins difficult to distinguish from secondary veins.

*Occurrence*: 10–3.8 Ma sedimentary rock formations at Tröllatunga (10 Ma), Stafholt, Þrimilsdalur (7–6 Ma) and Tjörnes (Skeifá, 3.9–3.8 Ma).

*Remarks*: Without epidermal structures preserved it is difficult to decide whether the leaves from Tröllatunga belong to this genus or not. Comparison with modern species, however, appears to support the generic identification. Beside *R. ponticum* from the southern and eastern Black Sea region, several eastern North American and East Asian large-leafed species belonging to *R.* subsection *Ponticum* (see Milne 2004 for circumscription of the group) closely resemble the fossils.

**cf. *Rhododendron* sp.** **M**

Plate 4.11, Fig.9.

2007a *Dicotylophyllum* sp. 2 ("*Rhododendron*" sp.) – Grímsson et al.: p. 207, pl. 9, figs. 1–2.
2007b *Rhododendron* sp. – Grímsson et al.: fig. 3, a.

Leaf, lamina narrow elliptic, entire, >7.0 cm long, 2.5 cm wide, length to width ratio ca 3.3, primary vein distinct, appearing grooved, secondary veins eucamptodromous to brochidodromous, >9 pairs of secondary veins, diverging from primary vein at angles of 55–50°.

*Occurrence*: 15 Ma sedimentary rock formation at Selárdalur.

*Remarks*: The single leaf recovered cannot unambiguously be assigned to the genus *Rhododendron*. The primary vein in this specimen is much narrower than the typical wide one found in the leaves from Tröllatunga. However, in modern species of *R.* subsection *Ponticum*, the primary vein forms a wide and distinct ridge on the abaxial side, whilst it is a narrow groove on the adaxial side.

***Rhododendron* sp. 1 [*R. ponticum* type]** **P**

Plate 4.11, Figs. 1–8; Plate 5.12; Figs. 8–11; Plate 10.15, Figs. 7–10.

Pollen, tetrad, diameter of tetrad 27–46 μm under SEM and 33–56 μm under LM, pollen tricolporate with small pori, colpi 11–14 μm long (SEM), tectate, columellate, pollen wall 1–1.8 μm thick (LM); sculpture microrugulate in aperture areas and apocolpi, microrugulae forming clusters separated by fossulae in the mesocolpium, microrugulae 0.2–0.8 μm long and 0.1–0.2 μm in diameter, viscin threads 0.3–0.5 μm in diameter (SEM).

*Occurrence*: 15–3.8 Ma sedimentary rock formations at Botn (15 Ma), Surtarbrandsgil (12 Ma) and Tjörnes (Egilsgjóta, Reká, Skeifá; 4.3–3.8 Ma).

*Remarks*: The exine sculpturing in this taxon is identical to the one found in the modern *R. ponticum* of Asia Minor and southwestern Europe. Other species in subsect. *Pontica* have a different exine sculpturing (T. Denk, pers. observ.; see Milne 2004 for circumscription of subsect. *Pontica*).

### *Rhododendron* sp. 2 P

Plate 5.12, Figs. 4–7; Plate 6.26, Figs. 1–8; Plate 7.12, Figs. 1–4; Plate 10.17, Figs. 1–3.

Pollen, tetrad, diameter of tetrad 23–48 μm under SEM and 31–60 μm under LM, pollen tricolporate with small pori, colpi 11–16 μm long (SEM), tectate, columellate, pollen wall 1–1.8 μm thick (LM); sculpture microverrucate in mesocolpium area, sculpture elements slightly elongated around apertures (microrugulate), in mesocolpium microverrucae forming clusters seperated by fossulae, microrugulate 0.1–0.3 μm long and 0.1–0.2 μm in diameter, viscin threads 0.3–0.4 μm in diameter (SEM), wider at point of attachment.

*Occurrence*: 12–4.0 Ma sedimentary rock formations at Surtarbrandsgil (12 Ma), Tröllatunga (10 Ma), Hrútagil (9–8 Ma) and Tjörnes (Reká, 4.2–4.0 Ma).

### *Vaccinium* sp. M

Plate 6.23, Figs. 4.7.

? 1886 *Vaccinium islandicum* Windisch – Windisch: p. 41, text-figs. 1–3.

Leaves petiolate; petiole 1.5 to >2 mm long, lamina elliptic, dentate, 1.6–3 cm long, 0.7–1.5 cm wide, length to width ratio 1.5–2.5, base rounded to acute, apex acute, secondary veins not clearly visible, teeth glandular, appressed, basal side much longer than apical side, at high magnification leaf surface densely beset with dark-shiny dots, which appear to be glands.

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

*Remarks*: Glands as found in the fossil leaves are typical of some evergreen species of *Vaccinium*. Windisch (1886) based his new species on two specimens (part and counterpart). His description fits well with the specimens described here. However, his line drawings show spinose teeth that are quite different from our specimens, and do not resemble Ericaceae.

### *Vaccinium* cf. *uliginosum* M

Plate 11.7, Figs. 1–2; Plate 11.22, Figs. 2–3; Plate 11.39, Fig. 2.

1978 *Vaccinium uliginosum* L. *fossilis* – Akhmetiev et al.: pl. 14, figs. 2, 4–6, 11.
1978 *Vaccinium uliginosum* L. *fossilis* – Akhmetiev et al.: pl. 15, fig. 6.

Leaf, petiole not preserved, lamina suborbicular, wide elliptic to obovate, 4–24 mm long, 3–20 mm wide, length to width ratio 1.2–2.1, base acute to obtuse, apex round

and in some cases notched, margin entire or in a few cases slightly revolute, 4–6 pairs of secondary veins, venation brochidodromous, primary loops followed by higher order loops, small ultimate loops along margin.

*Occurrence*: 3.9–0.8 sedimentary rock formations at Tjörnes (Skeifá, 3.9–3.8 Ma), Bakkabrúnir (1.7 Ma), Stöð (1.1 Ma) and Svínafell (0.8 Ma).

**Ericaceae gen. et spec. indet. 1** **P**

Plate 6.25, Figs. 1–6.

Pollen, tetrad, diameter of tetrad 26–38 μm under SEM and 29–46 μm under LM, pollen tricolporate, tectate, columellate, pollen wall ca 0.9–1.4 μm thick (LM); sculpture simple microrugulate around apertures, in mesocolpium microrugulae forming clusters seperated by fossulae (SEM).

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

**Ericaceae gen. et spec. indet. 2** **P**

Plate 9.11, Figs. 7–9.

Pollen, tetrad, diameter of tetrad 19–24 μm under SEM and 20–31 μm under LM, pollen tricolporate, tectate, columellate, pollen wall 1.5–2 μm thick (LM); sculpture rugulate to microrugulate, rugulae smooth and fused around apertures forming large islands separated by fossulae.

*Occurrence*: 5.5 Ma sedimentary rock formation at Selárgil.

**Ericaceae gen. et spec. indet. 3** **P**

Plate 9.12, Figs. 1–3.

Pollen, tetrad, diameter of tetrad 20–32 μm under SEM and 28–40 μm under LM, pollen tricolporate, tectate, columellate, pollen wall 1–3 μm thick (LM); sculpture rugulate to microrugulate, rugulae composed of rod-like elements, rods perpendicular to long axis of rugulae.

*Occurrence*: 5.5 Ma sedimentary rock formation at Selárgil.

**Ericaceae gen. et spec. indet. 4** **P**

Plate 10.17, Figs. 4–6.

Pollen, tetrad, diameter of tetrad 27–29 μm under SEM and 36–38 μm under LM, pollen tricolporate, tectate, columellate, pollen wall 1.7–1.8 μm thick (LM); sculpture microverrucate.

*Occurrence*: 4.3–4.2 Ma sedimentary rock formation at Tjörnes (Egilsgjóta).

**Ericaceae gen. et spec. indet. 5** **P**

Plate 10.17, Figs. 7–9.

Pollen, tetrad, diameter of tetrad 28–46 μm under SEM and 31–50 μm under LM, pollen tricolporate, tectate, columellate, pollen wall ca 1.8 μm thick (LM), markedly thicker in mesocolpium; sculpture microgemmate to gemmate, gemmae 0.3–1.1 μm in diameter, densely spaced, gemmae with microechinate suprasculpture.

*Occurrence*: 4.2–4.0 Ma sedimentary rock formation at Tjörnes (Reká).

**Ericaceae gen. et spec. indet. 6 [aff. *Empetrum nigrum* L.]** **P**

Plate 10.18, Figs. 1–3; Plate 11.23, Figs. 1–4; Plate 11.38, Figs. 1–3.

Pollen, tetrad, diameter of tetrad 21–31 μm under SEM and 26–43 μm under LM, pollen tricolporate, tectate, columellate, pollen wall 1–1.3 μm thick (LM); sculpture microechinate (SEM).

*Occurrence*: 4.2–0.8 Ma sedimentary rock formations at Tjörnes (Reká, 4.2–4.0 Ma), Stöð (1.1 Ma) and Svínafell (0.8 Ma).

**Ericaceae gen. et spec. indet. 7** **P**

Plate 10.18, Figs. 4–6.

Pollen, tetrad, diameter of tetrad 21–22 μm under SEM and 25–26 μm under LM, pollen tricolporate, tectate, columellate, pollen wall ca 0.8 μm thick (LM); sculpture striate-rugulate along colpi and in polar areas, rugulae forming clusters seperated by fossulae in mesocolpium.

*Occurrence*: 4.2–4.0 Ma sedimentary rock formation at Tjörnes (Reká).

**Ericaceae gen. et spec. indet. 8** **P**

Plate 11.8, Figs. 10–12.

Pollen, tetrad, diameter of tetrad 26–28 μm under SEM and 28–31 μm under LM, pollen tricolporate, tectate, columellate, pollen wall ca 0.8 μm thick (LM); sculpture verrucate, microverrucate, rugulate (SEM).

Occurrence: 1.7 Ma sedimentary rock formation at Bakkabrúnir.

**Ericaceae gen. et spec. indet. 9** **P**

Plate 11.38, Figs. 4–6.

Pollen, tetrad, diameter of tetrad 25–30 μm under SEM and 25–30 μm under LM, pollen tricolporate, tectate, columellate, pollen wall ca 1.2 μm thick (LM); sculpture microverrucate with a dense microechinate suprasculpture.

*Occurrence*: 0.8 Ma sedimentary rock formation at Svínafell.

## Euphorbiaceae

### *Euphorbia* sp. P

Plate 10.18, Figs. 7–9.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis 35–38 μm, equatorial diameter 22–34 μm under SEM, 43–46 μm and 26–42 μm under LM, tricolporate, colpi ca 27–29 μm long (SEM), 35–37 μm (LM); eutectate, columellate, pollen wall 1.6–2.2 μm thick (LM); sculpture perforate, foveolate, fossulate; distinct ectexine rim along colpi; aperture membrane covered with microverrucae and granulate elements (SEM).

*Occurrence*: 4.3–4.0 Ma sedimentary rock formations at Tjörnes (Egilsgjóta, Reká).

### *Mercurialis perennis* L. P

Plate 11.23, Figs. 5–7.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis 18 μm, equatorial diameter 12 μm under SEM, 21 μm and 19 μm under LM, tricolporate, colpi ca 15 μm long (SEM), 18 μm (LM); eutectate, columellate, pollen wall 0.6–0.8 μm thick (LM); sculpture microreticulate, muri microechinate (reticulum cristatum) (SEM).

*Occurrence*: 1.1 Ma sedimentary rock formation at Stöð.

## Fagaceae

### *Fagus friedrichii* Grímsson and Denk M

Plate 4.12, Figs. 7–13.

1946 *Fagus antipofii* Heer – Áskelsson: p. 81, fig. 2.
1946 *Fagus deucalionis* Unger – Áskelsson: p. 83, fig. 3.
1956 Dicotylodonae – Áskelsson: p. 46, fig. 4.
1957 *Fagus* cf. *ferruginea* Aiton – Áskelsson: p. 26, fig. 2.
1978 *Fagus* cf. *ferruginea* Aiton foss. Nathorst – Akhmetiev et al.: pl. 1, fig. 6.
1981 *Fagus* sp. – Friedrich and Símonarson: fig. 3.
2005 *Fagus friedrichii* Grímsson and Denk – Grímsson and Denk: p. 30, pl. 1–6.
2006 *Fagus friedrichii* Grímsson and Denk – Grímsson and Símonarson: p. 85, fig. 7–9.
2007a *Fagus friedrichii* Grímsson and Denk – Grímsson et al.: p. 193, pl. 6–8.

2007b *Fagus friedrichii* Grímsson and Denk – Grímsson et al.: fig. 3, b–k.
2008a *Fagus friedrichii* Grímsson and Denk – Grímsson and Símonarson: fig. 7.
2008b *Fagus friedrichii* Grímsson and Denk – Grímsson and Símonarson: fig. 3, E.

Leaf simple, petiolate; petiole 5–10 mm long, lamina 5.5–20.0 cm long, mean 12.7 cm, 2.4–12.1 cm wide, mean 6.3 cm, symmetrical or more rarely slightly asymmetrical and then one half of the leaf being wider than the other, wide to narrow elliptic, very rarely long ovate, obovate, or oblong; length to width ratio 1.4–2.8, mean 2.0, apex attenuate or acute, base mostly obtuse, to acute, and rarely cordate, primary vein straight, commonly having a zigzag course close to the apex, 15–20 pairs of secondaries, (4–)6–8 (−13) pairs per 5 cm, secondary veins in small leaves much more densely spaced than in larger (shade?) leaves, secondary veins craspedodromous, always running into a tooth, margin simple dentate, teeth with acute apex, basal side longer than apical side, the margin between two teeth being straight or sigmoid, teeth locally appressed, tertiary veins mainly perpendicular to secondary veins, simple or branching, 4–8 per 1 cm in large leaves (more than 15.0 cm long) and 6–16 in small leaves (5.0–10.0 cm long).

Cupules pedunculate, peduncle up to 2.1 cm long, 2–3 mm wide, distal part of peduncle slightly to markedly dilated, transitional part (connecting piece) short with sharp insertion; cupule 1.8–2.6 cm long and 1.0–1.7 cm wide, length to width ratio 1.25–1.86, narrow ovate, ovate to wide ovate, base round to acutely round; >20 appendages per valve, appendages widest at their base and gradually thinning towards pointed apex, pointing to the apex of the valve or recurved, regularly arranged on valves, present on basal part of the valve.

Nuts 1.2–1.7 cm long and 6–10 mm wide, length to width ratio 1.5–2.3, widest below the middle, narrow ovate (excluding wings), 3-angular, apex acute, narrowing into styles, base truncate, nuts with prominent wings; only one or two wings are visible due to compression of specimens, wings extending along upper two thirds of the margin.

*Occurrence*: 15–13.5 Ma sedimentary rock formations at Selárdalur, Botn (15 Ma) and Ketilseyri (13.5 Ma).

*Remarks*: Similar leaves have traditionally been assigned to *Fagus antipofii*. Grímsson and Denk (2005) showed that they differ substantially from the original material of *F. antipofii* from Central Asia and assigned them to *F. friedrichii*. Similarly large leaves with numerous secondary veins were described as *Fagus salnikovii* by Fotjanova (1988) from the Upper Oligocene to Lower Miocene of Sakhalin. They differ from *F. friedrichii* by their pseudocraspedodromous (to semicraspedodromous) venation, the widely spaced tertiary veins (in large leaves) and the very large leaf index. Another species from the Middle Miocene of Russia, *Fagus juliae* (Yakubovskaya 1975), superficially resembles *F. friedrichii* but differs from it by fewer secondary veins and displaying a range of secondary venation styles. *Fagus juliae* is preserved in very coarse sediment (pers. observation, T. Denk), which does not allow determination of the density of tertiary veins and, in most cases, the exact type of dentation. In addition, the Icelandic leaves are

conspicuously similar to leaves from the Middle Miocene of Idaho that have been called *Pseudofagus idahoensis* (Smiley and Huggins 1981). *Pseudofagus idahoensis* differs from *Fagus* in the regular occurrence of subsidiary teeth and the slightly larger number of secondary veins. It has not been reported beyond the type locality.

The fossil leaves most resemble the modern North American *F. grandifolia* Ehrh., although the way the secondary veins run into the teeth is much more variable in the modern species. Leaves similar to *Fagus friedrichii* can be found in some populations of the modern North American *Fagus grandifolia*. This applies to size and shape of the leaves, the high number of secondary veins, the prominently dentate leaf margin with craspedodromous venation, and commonly attenuate leaf apex. The modern *F. grandifolia*, however, displays great foliar variability (cf. Camp 1950) ranging from prominently dentate leaves to nearly entire margined ones that are very similar to the modern western Eurasian *Fagus sylvatica* (Shen 1992). By contrast, the nuts are conspicuously similar to those of the modern Japanese species *F. crenata* Blume (cf. Denk and Meller 2001). Denk and Grimm (2009b), based on a morphological-phylogenetic study, found that *F. friedrichii* is not distinctly similar to any modern species but more closely related to extinct types such as *F. idahoensis/F. washoensis* from the Middle Miocene of western North America. Since only one type of foliage, nuts, and cupules occur in the 15 Ma Selárdalur-Botn Formation we consider these to represent a single species, *Fagus friedrichii*.

### *Fagus friedrichii* Grímsson and Denk **P**

Plate 4.12, Figs. 1–6.

Pollen, monad, shape spheroidal, outline circular in equatorial view, polar axis 33–35 µm, equatorial diameter 28–34 µm under SEM, 38–42 µm and 33–42 µm under LM, tricolporate, colpi ca 25–35 µm long, eutectate, columellate, pollen wall 1.1–1.5 µm thick (LM); sculpture (micro)rugulate, rugulae smaller and narrower in polar region than in mesocolpium, rugulae with free-ending (protruding) rod-like portions (SEM).

*Occurrence*: 15 Ma sedimentary rock formation at Botn.

### *Fagus gussonii* Massalongo **M**

Plate 7.13, Figs. 1–4; Plate 7.14, Figs. 1–10; Plate 8.10, Figs. 1–2.

1972 *Fagus* sp. – Friedrich et al.: p. 8, pl. 1, fig. 3, 5, pl. 3, fig. 3.
1978 *Fagus orientalis* Lipsky – Akhmetiev et al.: pl. 8, fig. 10.
1978 *Fagus* sp.2 – Akhmetiev et al.: pl. 9, fig. 9.
1999c *Fagus antipofii* Heer – Denk: p. 634, pl. 2, fig. p.
2005 *Fagus gussonii* Massalongo – Grímsson and Denk: p. 43, pl. 10–13.
2005 *Fagus deucalionis* Unger emend. Denk and Meller – Grímsson and Denk: p. 50, pl. 12, figs. H–K, pl. 13, figs. B–D.

2005 *Fagus gussonii* Massalongo – Denk et al.: p. 388, figs. 97–102.
2006 *Fagus gussonii* Massalongo – Grímsson and Símonarson: p. 91, fig. 11–13.
2008a *Fagus gussonii* Massalongo – Grímsson and Símonarson: fig. 20.

Leaf simple, petiolate; petiole around 1–1.4 cm long in large leaves, as short as 3.0–4.5 mm in smaller leaves, lamina 5.0–17.5 cm long, mean 11.3 cm, 2.5–9.0 cm wide, mean 5.9 cm; symmetrical or asymmetrical, elliptic, wide elliptic to narrow obovate, in a few cases ovate to narrow ovate, length to width ratio 1.7–2.8, mean 1.9, leaves generally widest in the middle region of the lamina, rarely just below or above it, apex acute or acuminate, base acute to obtuse, in a few cases rounded or slightly cordate, in some specimens, basal part of lamina becoming convex thereby creating a distinct oblong region giving the leaf an inverted pear-shape; leaf margin crenulated or dentate; when present, the simple teeth occur along the whole margin or are restricted to the apical parts, basal and apical sides of teeth mostly convex, teeth with a long basal side and short apical side; primary vein straight to slightly curved, rarely displaying a zigzag course close to the apex, secondary venation typically pseudo- and semicraspedodromous, or craspedodromous, number of secondary veins (9–)10–13( to >16), regularly spaced, secondary veins diverging from midvein at an angle of 60–40° in the middle of the lamina (up to 83° at the base and down to 27° close to the apex), opadial veins locally present, (4–)5–7(−14) secondary veins per 5 cm, tertiary veins perpendicular to secondary veins and connecting adjacent secondary veins, simple or forked, approximately 4–6 tertiary veins per 1 cm of secondary vein (visible in two relatively large specimens only), quaternary veins relatively thick compared to the tertiary veins, and locally difficult to distinguish, course of the quaternary veins orthogonal, areoles well developed, oriented, quadrangular to hexagonal, no veinlets visible, marginal ultimate venation looped, the loops not reaching the margin.

Cupules stalked, pedunculate; peduncle 1.5–2.6 cm long, 1.75–2.30 mm wide, distal part of peduncle conspicuously thickened, dilated and gradually transitioning to the cupule (connecting piece); cupule valves (1.1–)1.4–2.0(−2.5) cm long, shape of valves wide elliptic to narrow elliptic or ovate to lanceolate, 20–35 appendages per valve, widest at their base and gradually thinning towards the pointed apex, appendages pointing to the apex of the valve or recurved, regularly arranged on the valves, absent from the basal part of the valve in some cases.

Nuts (8–)14–15.5 mm long and (4.5–)7.5–9 mm wide, length to width ratio 1.6–2.0, widest in the middle, elliptic to ovate-elliptic, 3-angular, apex acute, base truncate, nuts with wings; only one or two wings are visible due to compression of specimens, wings extending along upper two thirds of the margin.

*Occurrence*: 9–6 Ma sedimentary rock formations at Hrútagil (9–8 Ma) and Brekkuá (7–6 Ma).

*Remarks*: *Fagus gussonii* displays most morphological similarities to *Fagus sylvatica* L. from western Eurasia and *F. longipetiolata* Seemen from East Asia. *Fagus sylvatica* is a relatively polymorphic species and has been shown to incorporate several leaf morphotypes (Denk 1999a, b, c; Denk et al. 2002) as is the case with *F. gussonii*. The shape of leaves, size, margin, and venation type seen

in *F. gussonii* from Iceland corresponds with those found in *F. sylvatica* and to a lesser degree, with those found in the East Asian *F. longipetiolata* and *F. crenata* Blume. There is no other fossil *Fagus* species that is particularly similar to *F. gussonii*. The *F. gussonii* leaves are associated with relatively large cupules with spine-like appendages that are most similar to *Fagus sylvatica*, *F. crenata*, and *F. longipetiolata* among modern species (Shen 1992; Denk and Meller 2001).

***Fagus* sp.** **P**

Plate 6.27, Figs. 1–4; Plate 7.12, Figs. 5–10.

Pollen, monads or rarely in tetrads and clusters of up to 15, shape spheroidal, outline subcircular in equatorial view, polar axis 34–35 μm, equatorial diameter 28–29 μm under SEM, polar axis and equatorial diameter 37–38 and 30–40 μm under LM, tricolporate, colpi ca 26 μm long (SEM), ca 30 μm (LM), tectate, columellate, pollen wall 1.3–1.6 μm thick (LM), nexine thinner than sexine; sculpture rugulate, consisting of rod-like elements ≤ 1 μm long (SEM).

*Occurrence*: 10–8 Ma sedimentary rock formations at Tröllatunga (10 Ma) and Hrútagil (9–8 Ma).

***Trigonobalanopsis* sp.** **P**

Plate 6.27, Figs. 5–10; Plate 10.19, Figs. 1–6.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis 15–18 μm, equatorial diameter 9–12 μm under SEM, 15–23 and 11–14 μm under LM, tricolporate, colpi 13–15 μm long (SEM), 13–18 μm (LM), tectate, columellate, pollen wall 0.6–1 μm thick (LM), nexine relatively thinner than sexine; sculpture rugulate to microrugulate, perforate, irregularly arranged groups composed of parallel rugulae; rugulae 0.3–2.5 μm long, segmented; segments corresponding to subunits of rugulae (Claugher and Rowley 1990) (SEM).

*Occurrence*: 10–3.8 Ma sedimentary rock formations at Tröllatunga (10 Ma) and Tjörnes (Reká, Skeifá; 4.2–3.8 Ma).

***Quercus* infrageneric group *Quercus* sp. 1** **P**

Plate 7.14; Figs. 11–13.

2010 Pollen morphotype 1 – Denk et al.: p. 277, fig. 2 A–L.

Pollen monad, shape prolate, outline circular to lobate, pollen small to medium sized, polar axis 21–30 μm under LM, 18–28 μm under SEM, equatorial axis 18–25 μm under LM, 14–23 μm under SEM; tricolporoidate, colpi long and narrow, 16–25 μm under LM, 15–24 μm under SEM; tectate, columellate; sculpture verrucate to

microverrucate, basic units of verrucae are tuft-conglomerations sensu Rowley (1996) and Rowley and Gabarayeva (2004). Verrucae are of different size with diameters from <1 μm to >1 μm. The surface of verrucae is weakly bumpy. Tuft-conglomerations locally fuse to form larger verrucae in a cauliflower-like pattern (SEM).

*Occurrence*: 9–8 Ma sedimentary rock formation at Hrútagil.

*Remarks*: The fossil pollen shares the derived verrucate tectum ornamentation with pollen of modern white oaks (infrageneric group *Quercus*) and red oaks (infrageneric group *Lobatae*; Denk and Grimm 2009a). This synapomorphy suggests that the pollen from Iceland belongs to white or red oaks and indistinguishable pollen is found in modern North American, European and East Asian representatives of white oaks and in some red oaks, although the latter are more commonly perforate (Solomon 1983a, b; Denk and Grimm 2009a).

### *Quercus* infrageneric group *Quercus* sp. 2 P

Plate 9.12, Figs. 4–9.

2010 Pollen morphotype 2 – Denk et al.: p. 277, fig. 3 A–I.

Pollen monad, prolate, polar outline circular to lobate, equatorial outline circular to elliptic, pollen (small to) medium sized, polar axis 26–35 μm under LM, 22–31 μm under SEM, equatorial axis 20–26 μm under LM, 18–22 μm under SEM; tricolporoidate, colpi long and narrow, 20–30 μm under LM, 19–25 μm under SEM; pollen tectate, columellate; sculpture scabrate in LM, verrucate to microverrucate in SEM, basic units of verrucae are tuft–conglomerations sensu Rowley (1996) and Rowley and Gabarayeva (2004), verrucae of variable size with diameters from <1 μm to >1 μm, surface of verrucae appearing microechinate, each echinus representing the apical tip of a single tuft element forming the tuft-conglomerations or verrucae; tuft-conglomerations locally fusing to form larger verrucae.

*Occurrence*: 5.5 Ma sedimentary rock formation at Selárgil.

*Remarks:* The pattern of tectum ornamentation in the fossil pollen is also found in extant white oaks (infrageneric group *Quercus*) and red oaks (infrageneric group *Lobatae*). Among these groups, the observed vermiculate tectum ornamentation appears to be confined to North American species (Solomon 1983a, b). Although such types, to our knowledge, have not been reported from European strata, Liu et al. (2007) reported pollen with similar ornamentation from the Miocene of northeastern China, but these grains have a distinctly perforate tectum.

## Juglandaceae

For pollen morphology of modern Juglandaceae see, for example, Stone and Broome (1975) and Bos and Punt (1991).

***Carya* sp.** **P**

Plate 5.13, Figs. 1–3.

Pollen, monad, shape oblate, outline triangular in polar view, equatorial diameter 24–26 μm, under SEM, 27–28 μm under LM, triporate, porus diameter 1.4–1.5 μm, tectate, columellate, pollen wall ca 1.3 μm thick (LM); sculpture microechinate, microechinae densely and regularly spaced (SEM).

*Occurrence*: 12 Ma sedimentary rock formation at Surtarbrandsgil.

***Cyclocarya* sp.** **M**

Plate 6.28, Figs. 2–6; Plate 7.15, Fig. 6.

1991 *Carya* sp. – Símonarson: p. 144, fig. 1.
2005 cf. *Pterocarya* / *Cyclocarya* sp. – Denk et al.: p. 389, figs. 103–109, 112–114.

Leaflets, lamina elliptic, serrate, 6–16 cm long, 3–6 cm wide, base acute to asymmetrically rounded, apex acute, a large leaflet with petiolule preserved, petiolule ca 7 mm long, secondary venation semicraspedo-brochidodromous, primary loops followed by secondary loops from which veins run into teeth; teeth with long basal side and short apical side, tooth apex acute to acuminate; tertiary veins perpendicular to secondary veins close to the margin, oblique towards the midvein.

*Occurrence*: 10–6 Ma sedimentary rock formations at Tröllatunga, Húsavíkurkleif (10 Ma), Hrútagil (9–8 Ma) and Brekkuá (7–6 Ma).

*Remarks*: In a short note, Símonarson (1991) figured and described a leaflet from Tröllatunga as *Carya* sp. In general, species of *Pterocarya* and *Cyclocarya* commonly have semicraspedo-brochidodromous venation as found in the fossils, whereas secondaries in *Carya* and *Juglans* either split before reaching the margin, each branch supplying a tooth (craspedodromous), or form loops (brochidodromous to eucamptodromous) that reach almost to the margin, from which small tertiary veins run into the teeth. There are, however, some exceptions within *Carya* and *Juglans* with some species displaying some similarity to the fossils from Iceland. Among *Carya*, some *C. cathayensis* Sarg. show semicraspedo-brochidodromous venation with the loops not reaching close to the margin so that they are followed by second-order loops. The same is true for some specimens of *Juglans cinerea* L. Among *Pterocarya*, *P. fraxinifolia* Spach. has more widely spaced secondary veins and blunter teeth than the fossils, and primary loops reach closer to the margin. Several East Asian species are comparable with the fossil type (e.g. *P. rhoifolia* Sieb. and Zucc., *P. stenoptera* DC. and *P. tonkinensis* (Franch.) Dode). In addition, the Icelandic fossils resemble the Eurasian fossil species *Pterocarya paradisiaca* (Ung.) Iljinsk. and, to some extent, also *P. denticulata* (Weber) Heer (i.e. *Carya denticulata* (Weber) W. Schimper; cf. Dorofeev and Iljinskaja 1994). Ferguson (1971) pointed out the difficulties in trying to assign Juglandaceae-like leaves to a particular genus of the family and even to the family itself.

**cf. *Juglans* sp.** **M**

1868 *Juglans bilinica* Unger – Heer: p. 153, pl. 28, fig. 14.

Single leaf, lamina ca 13 cm long, 7.2 cm wide, >9 pairs of secondary veins, eucamptodromous, secondary veins running close towards margin, from secondary veins several small veins pass into small, sharp teeth (observed only in lower part of leaf).

*Occurrence*: 12 Ma sedimentary rock formation at Surtarbrandsgil.

*Remarks*: The single leaf reported by Heer and kept in the Copenhagen collection might indeed belong to *Juglans* although the determination is tentative. Among the living species of *Juglans*, leaves of *J. cathayensis* Dode resemble the fossil in their shape, course of secondary veins, and dentition.

***Pterocarya* sp.** **M**

Plate 6.28, Fig. 1; Plate 7.15, Fig. 1–5.

1972 *Pterocarya* sp. – Friedrich et al.: p. 9, pl. 2, figs. 1, 2.
1978 *Populus* sp. – Akhmetiev et al.: pl. 6, fig. 3.
1978 *Pterocarya paradisiaca* (Unger) Iljinskaya – Akhmetiev et al.: pl. 6, fig. 12.
1981 *Pterocarya* sp. – Friedrich and Símonarson: fig. 7.
2005 *Pterocarya* sp. – Grímsson et al.: p. 20, fig. 2, c–e.
2008a *Pterocarya* sp. – Grímsson and Símonarson: figs. 21–22.

Leaf, pinnately compound, one leaf with attached leaflets preserved, 14.5 cm long, 4 pairs of lateral leaflets and one terminal leaflet, the lowermost pair of leaflets much smaller than the remaining ones, leaflets shortly petiolate, 14–64 mm long, 6.5–20 mm wide; isolated leaflets up to 13.4 cm long, and 5.8 cm wide, length to width ratio 2.2–3.5, elliptic to narrow elliptic, base markedly asymmetrical, round in lateral leaflets, acute in terminal leaflets, apex acute, 12–18 pairs of secondary veins, lateral leaflets diverging from rhachis at angles of 75–45°, secondary venation eucamptodromous to brochidodromous, forming loops close to margin of lamina, leaf margin serrate, teeth small with acute apex, basal side convex, long, apical side straight to concave, short, small veins departing from secondary vein and running into teeth, tertiary veins percurrent, simple or forked, perpendicular to secondary veins, 5–8 tertiary veins per 1 cm secondary vein, quaternary veins forming an orthogonal pattern, areoles well developed, ultimate veinlets simple or branching once or twice.

Isolated fruit a nutlet with two lateral wings, wingspan 56 mm, nutlet pyramidal, wings in a single plane, nutlet 16 mm in diameter, wings subrhombic in outline, 28 mm long and 26.5 mm wide, numerous veins originating from nutlet and running towards the distal margin of the wing, veins dichotomising.

*Occurrence*: 12–8 Ma sedimentary rock formations at Seljá (12 Ma), Húsavíkurkleif (10 Ma) and Hrútagil (9–8 Ma).

*Remarks*: Leaves are very similar to the modern *P. fraxinifolia* (Lam.) Spach. from the eastern Black Sea and southern Caspian Sea areas. The large wings of the specimen

from Hrútagil are best comparable to some East Asian species of *Pterocarya*, such as *P. macroptera* Batalin *s.l.*

***Pterocarya* sp.** **P**

Plate 4.13, Figs. 1–6; Plate 5.13, Figs. 4–6; Plate 6.29, Figs. 1–6; Plate 7.16; Plate 10.19, Figs. 7–9.

Pollen, monad, shape oblate, outline subcircular to hexagonal in polar view, equatorial diameter 24–39 μm under SEM, 27–44 μm under LM, stephanopororate, six to nine pores, pori circular to elongated, 1.2–3.3 μm in diameter (SEM), tectate, columellate, pollen wall 1–1.6 μm thick (LM); sculpture microechinate, microechinae widely and regularly spaced (SEM).

*Occurrence*: 15–4.0 Ma sedimentary rock formations at Botn (15 Ma), Surtarbrandsgil (12 Ma), Tröllatunga, Húsavíkurkleif (10 Ma), Hrútagil (9–8 Ma) and Tjörnes (Egilsgjóta, Reká; 4.3–4.0 Ma).

*Remarks*: This morphotaxon may comprise more than one natural species.

**Haloragaceae**

***Myriophyllum* sp. 1** **P**

Plate 9.12, Figs. 10–12.

Pollen, monad, shape oblate, outline rounded to convex quadrangular in polar view, elliptic in equatorial view; equatorial diameter 21–22 μm under SEM, equatorial diameter 20–23 μm, polar axis ca 17 μm under LM, stephanopororate, 4 pori, pori elongate; tectate, columellate, pollen wall ca 1 μm thick (LM); sculpture perforate, foveolate and microechinate, microechinae arranged along foveolae (SEM).

*Occurrence*: 5.5 Ma sedimentary rock formation at Selárgil.

*Remarks*: Very similar pollen is found in the living species *Myriophyllum verticillatum* L. (Engel 1978).

***Myriophyllum* sp. 2** **P**

Plate 10.19, Figs. 10–12.

Pollen, monad, shape oblate, outline rounded to quadrangular in polar view, elliptic in equatorial view; equatorial diameter 17–18 μm under SEM, equatorial diameter ca 22 μm under LM, stephanopororate, four pori; tectate, columellate, pollen wall 1.3–1.7 μm thick (LM); sculpture verrucate with microechinae mostly around base of verrucae, perforate (SEM).

*Occurrence*: 4.2–4.0 Ma sedimentary rock formations at Tjörnes (Reká).

*Remarks*: Very similar pollen is found in the living species *Myriophyllum verticillatum* L. (Engel 1978).

## Lauraceae

### *Laurophyllum* sp. M

Plate 5.14, Figs. 1–2.

2005 *Laurophyllum* sp. 1 – Denk et al.: p. 392, figs. 207–208.

Lamina elliptic, entire, petiole not preserved, base acute, apex not preserved, ca 7 cm long, 2 cm wide, secondary venation eucamptodromous, six to eight pairs of secondary veins widely and irregularly spaced, the lowest pair more acute than pairs above; mesophyll tissue contains lens-shaped oil cells.

*Occurrence*: 12 Ma sedimentary rock formation at Surtarbrandsgil.

*Remarks*: Leaf shape and type of venation plus the presence of oil cells indicate closer affinity to Lauraceae. Foliage of the modern *Laurus nobilis* L. resembles the fossil leaf.

### *Sassafras ferrettianum* Mass. M

Plate 5.14, Figs. 3–6.

1954 *Sassafras* sp. – Áskelsson: p. 94, figs. 4–5.
1954 *Ficus* sp. – Áskelsson: p. 95, fig. 9.
1966 *Sassafras* sp. – Friedrich: p. 81, pl. 3, fig. 5, pl. 4, figs. 1, text-figs. 25–27.
1978 *Sassafras* sp. – Akhmetiev et al.: pl. 3, figs. 4–5.
2005 *Sassafras ferrettianum* Mass. – Denk et al.: p. 392, figs. 115–117.
2008a *Sassafras ferrettianum* Mass. – Grímsson and Símonarson: fig. 13.

Leaves, petiolate; petiole rarely preserved, lamina elliptic, wide elliptic or trilobed, symmetrical, margin entire, 5.8–19.5 cm long, 2.6–9.5 cm wide, length to width ratio 1.4–2.5, base cuneate to obtuse, apex bluntly acute, primary venation acrodromous in elliptic leaves, palinactinodromous in trilobed leaves, secondary venation camptodromous to brochidodromous. Oil cells 37–40 mm in diameter evident in mesophyll tissue of one specimen. No other details of epidermal tissue are available.

*Occurrence*: 12 Ma sedimentary rock formation at Surtarbrandsgil.

*Remarks*: *Sassafras* was a widespread element in the Cainozoic of Eurasia and North America. At present it comprises only three species displaying an East Asian-North American disjunction.

## Liliaceae

### Liliaceae gen. et spec. indet. 1 P

Plate 4.13, Figs. 7–12.

Pollen, monad, shape oblate, outline elliptic in polar view (boat shaped), polar axis 23–24 μm, equatorial diameter 28–32 μm under SEM, ca 25 μm and 32–35 μm

under LM, sulcate, semitectate, pollen wall thin, ca 0.6 μm thick (LM); sculpture heterobrochate reticulate, brochi gradually decreasing towards sulcus, pollen wall tectate perforate around sulcus (ca one-third of distal polar area), muri smooth, 0.3–0.4 μm wide (SEM).

*Occurrence*: 15 Ma sedimentary rock formation at Botn.

**Liliaceae gen. et spec. indet. 2** **P**

Plate 6.30, Figs. 1–3.

Pollen, monad, shape oblate, outline elliptic in polar view (boat shaped), polar axis ca 17 μm, equatorial diameter ca 38 μm under SEM, 20 μm and 46 μm under LM, sulcate, semitectate; sculpture heterobrochate reticulate, muri smooth, ca 0.5 μm wide, lumina decreasing towards apex (SEM).

*Occurrence*: 10 Ma sedimentary rock formation at Húsavíkurkleif.

**Liliaceae gen. et spec. indet. 3** **P**

Plate 6.29, Figs. 7–10; Plate 6.30, Figs. 4–7.

Pollen, monad, shape oblate, outline elliptic, equatorial diameter 25–40 μm under SEM, 27–42 μm under LM, sulcate, semitectate, pollen wall ca 1.2 μm thick (LM), sculpture heterobrochate reticulate, muri smooth, 0.2–0.6 μm wide, in some cases segments of muri relatively thin; brochi gradually decreasing towards sulcus, pollen wall tectate perforate around sulcus (ca one-fifth of distal polar area) (SEM).

*Occurrence*: 10 Ma sedimentary rock formation at Húsavíkurkleif.

**Liliaceae gen. et spec. indet. 4** **P**

Plate 9.13, Figs. 1–3.

Pollen, monad, shape oblate, outline elliptic, polar axis ca 18 μm, equatorial diameter ca 27 μm under SEM, ca 18 μm and ca 27 μm under LM, sulcate, semitectate, pollen wall ca 0.6 μm thick (LM), sculpture heterobrochate microreticulate, muri smooth, ca 0.4 μm wide (SEM).

*Occurrence*: 5.5 Ma sedimentary rock formation at Selárgil.

**Liliaceae gen. et spec. indet. 5** **P**

Plate 10.20, Figs. 1–5.

Pollen, monad, shape oblate, outline elliptic, polar axis ca 19 μm, equatorial diameter ca 31 μm under SEM, ca 23 μm and ca 37 μm under LM, sulcate, semitectate, pollen wall 0.5–0.7 μm thick (LM), sculpture heterobrochate reticulate, muri sometimes incomplete, 0.2–0.4 μm wide; brochi gradually decreasing towards apices, apices tectate perforate.

*Occurrence*: 4.3–3.8 Ma sedimentary rock formations at Tjörnes (Egilsgjóta, Skeifá; 4.3–3.8 Ma).

### Lythraceae

#### *Decodon* sp. P

Plate 6.31, Figs. 1–12.

Pollen, monad, shape subprolate, outline elliptic in equatorial view, polar axis 21–23 μm, equatorial axis 14–21 μm under SEM, 26–28 μm and 18–25 μm under LM, tricolporate, colpi 13–17 μm long (SEM), colpi commonly constricted in the area of endopori, rounded or truncated at distal ends, endopori small elliptic lalongate, tectate, columellate, pollen wall 1–1.5 μm thick, in the mesocolpium 2.5–4.2 μm wide meridional-ridges are running parallel to the colpi, sculpture (micro) verrucate/rugulate in mesocolpium, psilate in polar areas and on meridional ridges, in some cases meridional ridges with verrucate to rugulate sculpturing.

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga and Húsavíkurkleif.

### Magnoliaceae

#### *Liriodendron procaccinii* Unger M

Plate 5.15, Figs. 1–3.

1865 *Liriodendron procaccinii* Unger – Heer: p. 331, text-fig. 186 a, c.
1868 *Liriodendron procaccinii* Unger – Heer: p. 151, pl. 27, figs. 5–8.
2005 *Liriodendron procaccinii* Unger – Denk et al.: p. 392, fig. 124.
2008a *Liriodendron procaccinii* Unger – Grímsson and Símonarson: fig. 14.

Leaves petiolate; petiole partly preserved, >2.3 cm long, lamina four-lobed, 6.5–11.5 cm long, 9–14 cm wide, margin entire, secondary venation camptodromous to craspedodromous.

Samaroid fruits with a wing-like lanceolate style, 1.5–3 cm long, 2.5–4 mm wide; steep reticulate venation running from the pericarp towards the apex of the wing.

*Occurrence*: 12 Ma sedimentary rock formation at Surtarbrandsgil.

*Remarks*: The genus includes only two modern species, *L. tulipifera* L. in North America and *L. chinensis* Sargent in Central China. *Liriodendron* was a common element in the Cainozoic of the Northern Hemisphere. In Europe it persisted at least until the Late Pliocene (cf. Knobloch 1998).

#### cf. *Magnolia* sp. M

1978 *Magnolia* sp. – Akhmetiev et al.: pl. 1, fig. 7.
2007a *Magnolia* sp. – Grímsson et al.: p. 197, pl. 9, figs. 3, 4.

2007b *Magnolia* sp. – Grímsson et al.: fig. 7, a.

Leaf pinnate, lamina estimated 9.0 cm long, 4.0 cm wide, elliptic to narrow obovate, symmetrical, margin entire, primary vein straight, moderately thick to stout, secondary venation brochidodromous, >7 pairs of alternately arranged secondary veins, diverging from midvein at angles of 60–71°, forming loops, primary loops followed by secondary loops, 0–2 intersecondary veins.

*Occurrence*: 15 Ma sedimentary rock formation at Selárdalur.

### *Magnolia* sp. M

Plate 5.15, Figs. 4–8.

1956 Magnoliaceae – Áskelsson: p. 45, figs. 2a–b.
1966 *Magnolia* cf. *reticulata* Chaney and Sanborn – Friedrich: p. 78, pl. 3, figs. 1–4, text-figs. 23–24.
1978 *Magnolia* sp. – Akhmetiev et al.: pl. 4, fig. 1a.
2005 ? *Magnolia* sp. – Denk et al.: p. 392, figs. 115–118.
2008a *Magnolia* sp.– Grímsson and Símonarson: fig. 12.

Leaves, no petiole preserved, lamina elliptic to obovate, entire, 8–21 cm long, 2.5–7 cm wide, base rounded to bluntly acute or very-base oblong, apex acute, secondary venation brochidodromous, 9–18 pairs of secondary veins. Cuticle structure is the same in very large and much smaller leaves, suggesting a large size range within the species; anticlinal walls of cells are finely undulating both on the adaxial and abaxial leaf side; on a fragment of the costal area, dense rounded simple serial trichome bases are present, rarely with an attached long terminal part.

Seed possibly belonging to *Magnolia*, 6.5 mm long, 5.3 mm wide, length to width ration 1.2, outline tear shaped.

*Occurrence*: 12 Ma sedimentary rock formation at Surtarbrandsgil and Seljá.

*Remarks*: Such leaves closely resemble species of *Magnolia* L. (East Asia-Himalayas, North and Central America), *Michelia* L. and *Manglietia* Blume (both East Asia). The cuticle features of this type are known from some Magnoliaceae, particularly *Michelia* and some species of *Magnolia* (Baranova 1972). However, the oil cells widely spread in the Magnoliaceae have not been observed in the material at hand.

## Menyanthaceae

### *Menyanthes* sp. P

Plate 9.13, Figs. 4–6; Plate 10.20, Figs. 6–8; Plate 11.9, Figs. 1–3; Plate 11.38, Figs. 7–12.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis 11–15 μm, equatorial diameter 6–10 μm under SEM, 13–16 μm and 8–12 μm under LM, tricolporate, colpi 10–12 μm long (SEM), 10–13 μm (LM); tectate,

columellate, pollen wall 0.7–1.2 μm thick (LM); sculpture striate, striae not oriented, 0.3–2.6 μm long, area between striae variable in size and shape (SEM).

*Occurrence*: 5.5–0.8 Ma sedimentary rock formations at Selárgil (5.5 Ma), Tjörnes (Reká, 4.2–4.0 Ma), Bakkabrúnir (1.7 Ma) and Svínafell (0.8 Ma).

Remarks: This pollen is similar to modern species of *Menyanthes* (see, for example, Nilsson 1973; Blackmore and Heath 1984).

## Myricaceae

### *Comptonia hesperia* Berry M

Plate 5.16, Figs. 1–5.

1966 *Comptonia hesperia* Berry – Friedrich: p. 68, pl. 1, figs. 1, 2, 4, text-fig. 17.
2005 Pteridophyta gen. et spec. indet 2 ("*Dryopteris*" sp.) – Denk et al.: p. 373, figs. 12–13.
2005 *Comptonia hesperia* Berry – Denk et al.: p. 392, figs. 125–126.
2008a *Comptonia hesperia* Berry – Grímsson and Símonarson: fig. 15.

Leaves elliptic, dissected, sessile, fern-like, 3–5 cm long and 1.4–1.6 cm wide, becoming narrower towards the apex, base decurrent, apex rounded, each lobe of the leaf supplied by 2–3 secondary veins, lobes oblong to triangular, maximally 1 cm long and 4 mm wide, forming an angle of about 30–45° with primary vein, not fused at base or fused along ≤ ¼ of their length (mostly in basal or apical part of lamina), sinus between the lobes rounded to acute, apex of lobe acute.

*Occurrence*: 12 Ma sedimentary rock formation at Surtarbrandsgil.

*Remarks*: These leaf remains are also similar to narrow forms of *C. oeningensis* A. Braun [~ *Myrica oeningensis* (A. Braun) Heer], which differs in producing incompletely dissected leaves ('*vindobonesis*'-type). According to Zhilin (1980) and Friedrich (1966), it is extremely difficult to assess specific relationships of fossil *Comptonia* on the basis of few fragments without knowing the range of variation in the populations under study.

### *Myrica* sp. P

Plate 7.16, Figs. 7–12; Plate 10.20, Figs. 9–11; Plate 11.9, Figs. 4–9.

Pollen, monad, shape spheroidal, outline convex triangular in polar view, equatorial diameter 21–38 μm under SEM, and 22–44 μm under LM, angulaperturate, triporate, rarely tetraporate, porus 1.3–2 μm in diameter (SEM), annulate, atrium between ectopore and endopore (LM), tectate, columellate, pollen wall 1.2–1.7 μm thick (LM); sculpture microechinate, microechinae wide at base (SEM).

*Occurrence*: 9–1.7 Ma sedimentary rock formations at Hrútagil (9–8 Ma), Tjörnes (Egilsgjóta, Reká, Skeifá; 4.3–3.8 Ma) and Bakkabrúnir (1.7 Ma).

## Nymphaeaceae

### *Nuphar* sp. P

Plate 9.13, Figs. 7–9.

Pollen, monad, shape oblate (boat shaped), outline subcircular, diameter 41–47 under SEM, and 39–48 μm under LM, sulcate, tectate, columellate, pollen wall 1.8 μm thick (LM); sculpture echinate, microrugulate/rugulate, echinae irregularly spaced, 4.8–5.5 μm high, 2–2.2 μm wide at base (SEM).

*Occurrence*: 5.5 Ma sedimentary rock formation at Selárgil.

*Remarks*: Pollen of the modern species *Nuphar lutea* (L.) Sm. is very similar to the fossil one (Jones and Clarke 1981).

### cf. *Nuphar* sp. M

Plate 6.32, Figs. 1–2.

2005 ? *Nuphar* sp. – Denk et al.: p. 404, figs. 198–199.

Fragments of large round leaves showing some details of venation may belong to an aquatic plant. Similar leaves occur in *Nuphar* Sm., where secondaries run radially from the leaf base and pinnately from the primary vein with higher order veins running parallel and perpendicular between the secondary veins.

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

## Oleaceae

### cf. *Fraxinus* sp. M

Plate 5.16, Fig. 6.

2007a Incertae sedis no. 3 ("*Fraxinus*" sp.) – Grímsson et al.: p. 207, pl. 17, fig. 2.
2007b *Fraxinus* sp. – Grímsson et al.: fig. 3, l.

Samara, >2.6 cm long, 4.4 mm wide, wing with parallel running veins, distal part of wing missing.

*Occurrence*: 12 Ma sedimentary rock formation at Surtarbrandsgil.

## Onagraceae

### *Epilobium* sp. P

Plate 10.21, Figs. 1–3.

Pollen, monad, shape oblate, outline convex triangular in polar view, equatorial diameter 43–51 μm under SEM, 57–63 μm under LM, triporate, pores and annulus

oriented distally, annulus prominent, 12.8–15.7 μm wide; pollen wall 2.5–3 μm thick (LM); sculpture microrugulate, rugulate-striate around pores, viscin threads on proximal side.

*Occurrence*: 4.2–4.0 Ma sedimentary rock formation at Tjörnes (Reká).

*Remarks*: Very similar tectum ornamentation and viscin threads have been figured by Praglowski et al. (1994).

**Onagraceae gen. et spec. indet.** **P**

Plate 11.24, Figs. 1–4.

Pollen, monad, shape oblate, outline convex triangular in polar view, equatorial diameter 34—49 μm under SEM, 42–60 μm under LM, triporate, pores oriented distally; pollen wall 1.8 μm thick (LM); sculpture microrugulate, viscin threads on proximal side.

*Occurrence*: 1.1 Ma sedimentary rock formation at Stöð.

*Remarks*: Similar tectum ornamentation and viscin threads have been figured by Praglowski et al. (1987, 1994).

**Plantaginaceae**

***Plantago lanceolata* L.** **P**

Plate 6.32, Figs. 3–6; Plate 9.13, Figs. 10–12.

Pollen, monad, shape spheroidal, outline circular, diameter 17–19 μm under SEM, 21–23 μm under LM, pantoporate, pore diameter (lumen) 1.5–2.6 μm, aperture with complete operculum, annulate, annulus 1–1.9 μm wide, pollen wall 1–1.4 μm thick (LM); sculpture perforate, weakly verrucate, verrucae ca 1 μm in diameter, with microechinate suprasculpture, microechinae equally spaced (SEM).

*Occurrence*: 10–5.5 Ma sedimentary rock formation at Tröllatunga (10 Ma) and Selárgil (5.5 Ma).

*Remarks*: Pollen very similar to the fossil one is figured in Clarke and Jones (1977a).

***Plantago coronopus* L.** **P**

Plate 10.21, Figs. 4–6; Plate 11.23, Figs. 8–10.

Pollen, monad, shape spheroidal, outline circular, diameter 13–18 μm under SEM, 15–22 μm under LM, pantoporate, pore diameter (lumen) 1.1–2.4 μm, aperture membrane (operculum) microechinate, annulate, annulus very prominent, 2 μm wide ; pollen wall 1.7 μm thick (LM), sculpture perforate, verrucate, verrucae covered with microechinae; microechinae equally spaced.

*Occurrence*: 4.2–1.1 Ma sedimentary rock formation at Tjörnes (Reká, 4.2–4.0 Ma) and Stöð (1.1 Ma).

*Remarks*: Pollen very similar to the fossil one is figured in Clarke and Jones (1977a).

## Platanaceae

### *Platanus leucophylla* (Unger) Knobloch M

Plate 4.14, Fig. 9.

2007a *Platanus leucophylla* (Unger) Knobloch – Grímsson et al.: p. 200, pl. 10.
2007b *Platanus leucophylla* (Unger) Knobloch – Grímsson et al.: fig. 7, c–d.

Lamina palmate, three-lobed, preserved part 8.7 cm long and 5.2 cm wide, estimated size 12.0 cm long, 7.4 cm wide, length to width ratio 1.62, base obtuse, cuneate to decurrent; margin dentate, apical side of tooth straight to concave, basal side straight, sinuses between teeth round, secondary veins serving simple, widely spaced teeth; primary venation palinactinodromous, five primary veins, radiation suprabasinal, primary veins perfect and marginal, weak to moderate in thickness, middle vein thickest, lateral primary veins next to base thinner than upper ones; secondary venation craspedodromous, upper lateral primary veins arising at narrow angles (close to 36°) from primary midvein, second pair arising at moderate angles (close to 52°) from midvein, secondary veins diverging from central primary vein at 35–45°, thin basal marginal vein (opadial vein) present; tertiary vein pattern percurrent, forked, in some cases simple, convex, approximately 3–5 tertiary veins per cm of primary or secondary vein, forming acute angles at both abmedial and admedial sides of secondary veins; quaternary veins orthogonal.

*Occurrence*: 15 Ma sedimentary rock formation at Selárdalur.

*Remarks*: This *Platanus* foliage is strikingly similar to the living North American species *P. occidentalis* L. subsp. *occidentalis* and subsp. *palmeri* (Kuntze) Nixon and Poole ex Geerinck, and to the widely planted hybrid *P.* x *hispanica* Miller ex Münchh. (*P. occidentalis* x *orientalis*), based on leaf shape and the few elongate teeth (cf. Nixon and Poole 2004). Similar leaves have been reported from Miocene deposits of Europe and North America (e.g., Chaney and Elias 1936).

### *Platanus* sp. P

Plate 4.14, Figs. 1–8; Plate 5.13, Figs. 10–12; Plate 6.32, Figs. 6–8.

Pollen, monad, shape subprolate, outline elliptic in equatorial view, polar axis 17–20 μm, equatorial diameter 11–16 μm under SEM, 18–22 μm and 12–18 μm under LM, tricolpate, colpi 9–16 μm long and 2.1 μm wide (SEM), 15 μm long under LM, semitectate, columellate, pollen wall 0.8–1.7 μm thick (LM); sculpture

microreticulate, crests of muri "crown-like", aperture membrane covered with non-continuous elements (microverrucae) of the ectexine (SEM).

*Occurrence*: 15–10 Ma sedimentary rock formations at Botn (15 Ma), Surtarbrandsgil (12 Ma), Tröllatunga and Húsavíkurkleif (10 Ma).

**Poaceae**

***Phragmites* sp.** **M**

Plate 6.33, Figs. 1–2 ; Plate 8.10, Figs. 3–4.

1978 *Phragmites oeningensis* A. Braun – Akhmetiev et al.: pl. 6, fig. 4.

Leaves, rhizomes; sheaths and blades of leaves; stems or rhizomes with distinct nodes and internodes typical for the genus.

*Occurrence*: 12–3.8 Ma sedimentary rock formations at Surtarbrandsgil, Seljá (12 Ma), Brekkuá (7–6 Ma), Selárgil (5.5 Ma) and Tjörnes (Reká, Skeifá; 4.2–3.8 Ma).

**Poaceae gen. et spec. indet. 1** **P**

Plate 6.33, Figs. 3–8 ; Plate 7.17, Figs. 1–3 ; Plate 10.21, Figs. 7–9 ; Plate 11.24, Figs. 5–7 ; Plate 11.40 ; Figs. 1–3.

Pollen, monad, shape spheroidal, outline circular to elliptic, diameter 17–31 μm under SEM, 19–37 μm under LM, ulcerate, ulcus 0.8–2.9 μm in diameter, operculum microechinate; annulate; eutectate, pollen wall 0.8–1 μm thick (LM), sculpture microareolate, islands relatively small, microechinate.

*Occurrence*: 10–0.8 Ma sedimentary rock formations at Tröllatunga (10 Ma), Hrútagil (9–8 Ma), Tjörnes (Skeifá, 3.9–3.8 Ma), Stöð (1.1 Ma) and Svínafell (0.8 Ma).

**Poaceae gen. et spec. indet. 2** **P**

Plate 9.14, Figs. 1–3.

Pollen, monad, shape spheroidal, outline elliptic, polar axis 59 μm, equatorial axis 45 μm under LM, ulcerate, ulcus 2.4–3 μm in diameter (SEM), annulate; eutectate, sculpture microechinate, microechinae regularly spaced, with a circular base, 0.5 μm in diameter (SEM).

*Occurrence*: 5.5 Ma sedimentary rock formation at Selárgil.

**Poaceae gen. et spec. indet. 3** **P**

Plate 10.21, Figs. 10–12.

Pollen, monad, shape ellipsoidal, outline elliptic, diameter 21–39 μm under SEM, 25–44 μm under LM, ulcerate, ulcus 1.5–1.7 μm in diameter, annulate; eutectate,

pollen wall 0.7 μm thick (LM), sculpture microareolate, islands relatively large, microechinate.

*Occurrence*: 4.3–4.0 Ma sedimentary rock formations at Tjörnes (Egilsgjóta, Reká).

**Poaceae gen. et spec. indet. 4** **P**

Plate 11.24, Figs. 8–10; Plate 11.40, Figs. 4–6.

Pollen, monad, shape spheroidal, outline circular, diameter 24–32 μm under (SEM), 25–33 μm under LM, ulcerate, ulcus 1.6–3.3 μm in diameter (SEM), annulate; eutectate, pollen wall 0.6–1.3 μm thick (LM), sculpture microareolate, areolae widely spaced, irregular outline, microechinate, fossulae between areolae distinctly perforate.

*Occurrence*: 1.1–0.8 Ma sedimentary rock formations at Stöð (1.1 Ma) and Svínafell (0.8 Ma).

**Poaceae gen. et spec. indet. 5** **P**

Plate 11.40, Figs. 7–9.

Pollen, monad, shape ellipsoidal, outline elliptic, diameter 25–49 μm under (SEM), 27–47 μm under LM, ulcerate, ulcus 2.6–3.3 μm in diameter (SEM), annulate; eutectate, pollen wall 1.3 μm thick (LM), sculpture microechinate, microechinae regularly and densely spaced, with a polygonal base, small, ≤0.3 μm in diameter.

*Occurrence*: 0.8 Ma sedimentary rock formation at Svínafell.

**Poaceae gen. et spec. indet. 6** **P**

Plate 11.40, Figs. 10–12.

Pollen, monad, shape spheroidal, outline circular, diameter 20–26 μm under (SEM), 22–29 μm under LM, ulcerate, ulcus 1.2–1.4 μm in diameter (SEM), annulate; eutectate, pollen wall 1.5 μm thick (LM), sculpture microareolate, distinctly fossulate, areolae regularly spaced, polygonal in outline, areolae microechinate.

*Occurrence*: 0.8 Ma sedimentary rock formation at Svínafell.

**Poales**

**Poales fam. gen. et spec. indet.** **M**

Plate 11.22, Fig. 4; 11.39, Fig. 3

Fragments of axes and/or leaves, showing parallel venation, up to 4.0 cm long and 1–5 mm wide.

*Occurrence*: 5.5–0.8 Ma sedimentary rock formations at Selárgil (5.5 Ma), Stöð (1.1 Ma) and Svínafell (0.8 Ma).

**Polygonaceae**

***Rumex* sp.** **P**

Plate 6.32, Figs. 9–11; Plate 10.22, Figs. 1–3; Plate 11.10, Figs. 4–6; Plate 11.25, Figs. 7–9; Plate 11.41, Figs. 4–6.

Pollen, monad, shape prolate, outline circular in polar view, polar axis 26–32 μm, equatorial diameter 16–31 μm under SEM, polar axis 18–38 μm, equatorial axis 18–40 μm under LM, tricolporate, colpi 21–23 μm long (SEM), 11–28 μm (LM); eutectate, columellate, pollen wall 1.2 μm thick (LM); sculpture foveolate, microechinate, perforate.

*Occurrence*: 10–0.8 Ma sedimentary rock formations at Tröllatunga (10 Ma), Tjörnes (Reká, 4.2–4.0 Ma), Bakkabrúnir (1.7 Ma), Stöð (1.1 Ma) and Svínafell (0.8 Ma).

***Persicaria* sp. 1** **P**

Plate 8.11, Figs. 1–3.

Pollen, monad, shape spheroidal, outline circular, diameter 39–47 μm under SEM, 50–57 μm in LM, pantoporate, semitectate, columellate; sculpture heterobrochate reticulate, smooth muri supported by two rows of columellae (SEM).

*Occurrence*: 7–6 Ma sedimentary rock formation at Hestabrekkur.

*Remarks*: Various species of *Persicaria* show similar sculpturing and arrangement of apertures (Van Leeuwen et al. 1988; Hong 1993).

***Persicaria* sp. 2** **P**

Plate 10.22, Figs. 4–6.

Pollen, monad, shape spheroidal, outline circular, diameter ca 53 μm under SEM, ca 60 μm in LM, pantocolpate, colpi short, ca 4 μm (SEM); semitectate, columellate, pollen wall ca 3 μm thick (LM); sculpture heterobrochate reticulate, smooth muri, muri often undulating, sometimes segmented, muri supported by two rows of columellae (SEM).

*Occurrence*: 4.2–4.0 Ma sedimentary rock formations at Tjörnes (Reká).

*Remarks*: Various species of *Persicaria* have very similar sculpturing and type and arrangement of apertures (Van Leeuwen et al. 1988; Hong 1993).

***Polygonum aviculare* L.** **P**

Plate 11.25, Figs. 1–3.

Pollen, monad, shape prolate, outline lobate in polar view, elliptic in equatorial view, polar axis 16–21 μm, equatorial diameter 12–17 μm under SEM, 23–26 μm and 14–21 μm under LM; tricolporate, colpi 13–17 μm long (SEM), 16–20 μm (LM); columellate, pollen wall 1.8 μm thick (LM), sculpture perforate-microechinate.

*Occurrence*: 1.1 Ma sedimentary rock formation at Stöð.

*Remarks*: The fossil grains are indistinguishable from the modern species (cf. Van Leeuwen et al. 1988).

### ***Polygonum viviparum* L.** **P**

Plate 10.22, Figs. 7–9; Plate 11.10, Figs. 1–3; Plate 11.25, Figs. 4–6; Plate 11.41, Figs. 1–3.

Pollen, monad, shape prolate, outline lobate in polar view, elliptic in equatorial view, polar axis 17–52 μm, equatorial diameter 16–32 μm under SEM, 18–61 μm and 16–42 μm under LM; tricolporate, colpi 14–35 μm long (SEM), 18–37 μm (LM); columellate, pollen wall 2.7 μm thick (SEM), 1.6–3.3 μm (LM) (thickest at the poles), sculpture perforate-microechinate, perforations markedly larger in polar area.

*Occurrence*: 5.5–0.8 Ma sedimentary rock formations at Selárgil (5.5 Ma), Tjörnes (Egilsgjóta, Reká, Skeifá; 4.3–3.8 Ma), Bakkabrúnir (1.7 Ma), Stöð (1.1 Ma) and Svínafell (0.8 Ma).

*Remarks*: This pollen type shows great variability in size and shape, ranging from oblate to rounded and prolate. The fossil grains are indistinguishable from the modern species (cf. Van Leeuwen et al. 1988).

### ***Polygonum viviparum* L.** **M**

Plate 11.7, Fig. 3; Plate 11.22, Figs. 5–8; Plate 11.39, Figs. 4–6.

1978 *Polygonum (Bistorta) viviparum* L. foss. – Akhmetiev et al.: pl. 15, fig. 11; pl. 16, figs. 4, 12–15, 19–21.

Leaves, petiolate; petiole rarely preserved, up to 3 mm long, lamina 1.4–6 cm long, 3.6–20 mm wide, length to width ratio 1.9–6.9, lamina symmetrical, base commonly asymmetrical, elliptic, narrow elliptic to lorate, apex acute, base acute, margin entire, revolute, each side of primary vein typically flanked by a longitudinal furrow, secondary venation relatively thin compared to primary vein, reticulodromous, many veins originating at irregular intervals from primary vein, curving upwards, repeatedly branching and re-joining, close to margin all branches turning towards margin and entering margin at a right angle.

*Occurrence*: 1.7–0.8 Ma sedimentary rock formations at Bakkabrúnir (1.7 Ma), Stöð (1.1 Ma) and Svínafell (0.8 Ma).

*Remarks*: Dimorphic short elliptic and lorate leaves represent outer and inner rosette leaves, respectively. This is also observed in modern representatives of the species.

***Polygonum* sect. *Aconogonon* sp.** **P**

Plate 6.34, Figs. 13–15; Plate 11.10, Figs. 7–9.

Pollen, monad, shape spheroidal, diameter 8–14 μm under SEM, 10–18 μm under LM, pantoporate, 12 pori; eutectate, columellate, pollen wall 0.7–1.4 μm thick (LM), sculpture microechinate.

*Occurrence*: 10–1.7 Ma sedimentary rock formations at Tröllatunga (10 Ma) and Bakkabrúnir (1.7 Ma).

*Remarks*: Similar grains have been described by Hong and Hedberg (1990).

**Potamogetonaceae**

***Potamogeton* sp.** **M**

Plate 10.23, Figs. 1–2.

1978 *Potamogeton* sp. 1 – Akhmetiev et al.: pl. 12, fig. 14.

Leaves, petiolate; preserved part of petiole 7 mm long, lamina elliptic, 6.5–8 cm long, 2.1–2.5 cm wide, base obtuse, margin entire, central primary vein flanked on each side by two lateral primary veins, two or three weaker veins running between two adjacent primary veins, these veins converging apically, tertiary veins simple or forked perpendicular to primary veins, 9–12 tertiary veins per 5 mm of primary vein.

*Occurrence*: 3.9–3.8 Ma sedimentary rock formation at Tjörnes (Skeifá).

**Ranunculaceae**

The pollen morphology of living members of the family has been described by Santisuk (1979) and Clarke et al. (1991), among others.

***Anemone* sp.** **P**

Plate 6.33, Figs. 9–11.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis 29 μm, equatorial diameter 20 μm under SEM, 35 μm and 21 μm under LM, tricolpate, colpi 19 μm long, eutectate, columellate, pollen wall 0.6–1.3 μm thick (LM), sculpture perforate-microechinate, 13 echinae per 50 $\mu m^2$ (SEM).

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

***Ranunculus* sp. 1** **P**

Plate 6.34, Figs. 10–12; Plate 9.14, Figs. 7–9; Plate 10.24, Figs. 4–6.

Pollen, monad, shape spheroidal, outline subcircular, diameter 23–32 μm under SEM, 25–37 μm under LM, pantocolpate, colpi short, 4.8–10 μm long (SEM), 8–10 μm (LM); eutectate, columellate, pollen wall 1–2 μm thick (LM), sculpture perforate, microechinate; microechinae evenly spaced, ca 20–37 per 50 $\mu m^2$ tectum, colpus rim and colpus membrane densely covered with microechinae (SEM).

*Occurrence*: 10–4.0 Ma sedimentary rock formation at Tröllatunga (10 Ma), Selárgil (5.5 Ma) and Tjörnes (Reká, 4.2–4.0 Ma).

*Remarks*: Similar to *R. falcatus* L. figured by Santisuk (1979).

***Ranunculus* sp. 2** **P**

Plate 9.14, Figs. 10–12; Plate 10.24, Figs. 7–9.

Pollen, monad, shape prolate, outline in equatorial view elliptic, polar axis 21–25 μm, equatorial diameter 16–18 μm under SEM, 22–28 and 18–21 μm under LM, tricolpate, colpi 15–20 μm long (SEM), 16–22 μm (LM); eutectate, columellate, pollen wall ca 0.8 μm thick (LM), sculpture perforate, microechinate; microechinae conical with wide base, locally clustering, 11–29 per 50 $\mu m^2$ tectum; markedly smaller microechinae rarely present between microechinae (SEM).

*Occurrence*: 5.5–4.2 Ma sedimentary rock formations at Selárgil (5.5 Ma) and Tjörnes (Egilsgjóta; 4.3–4.2 Ma).

***Ranunculus* sp. 3** **P**

Plate 11.10, Figs. 10–12.

Pollen, monad, shape prolate to spheroidal, outline elliptic in equatorial view, equatorial diameter 17–18 μm under SEM, 19–20 μm under LM, tricolpate; eutectate, columellate, pollen wall 0.8 μm thick (LM), sculpture finely perforate, microechinate; microechinae commonly clustering on elevated islands, 45 microechinae per 50 $\mu m^2$ tectum (SEM).

*Occurrence*: 1.7 Ma sedimentary rock formation at Bakkabrúnir.

***Ranunculus* sp. A** **M**

Plate 11.42, Figs. 1–4; Plate 11.43, Fig. 1.

Leaf, palmately and shallowly lobed, no petiole preserved, lamina 3.2–6.6 cm long, 4.0–7.2 cm wide, length to width ratio 0.8–0.9, lamina symmetrical, wide ovate, apex rounded, base cordate to deeply cordate, auriculate, margin serrate, teeth with convex basal and apical sides, regularly spaced and of equal size, primary venation actinodromous to palinactinodromous, in a complete specimen seven primary veins, slightly curved, primary veins sending off several secondary veins, secondary

venation craspedodromous to camptodromous, secondary veins branching and some branches supplying teeth, others joining adjacent primary or secondary veins, secondary veins diverging from primary vein at steep angles, three to four pairs per primary vein, tertiary venation percurrent, forked, few veins wide apart.

*Occurrence*: 0.8 Ma sedimentary rock formation at Svínafell.

### *Thalictrum* sp. 1 P

Plate 6.21, Figs. 5–10; Plate 9.15, Figs. 1–3.

Pollen, monad, shape spheroidal, outline circular, diameter 11–17 μm under SEM and 12–19 μm under LM, pantoporate, tectate, columellate, pollen wall 1.4 μm thick (LM), sculpture microechinate, microechinae densely spaced, 85–90 per 50 $\mu m^2$, aperture membrane densely covered with microechinae of different size, 350–600 μm (SEM).

*Occurrence*: 10–5.5 Ma sedimentary rock formations at Tröllatunga (10 Ma) and Selárgil (5.5 Ma).

### *Thalictrum* sp. 2 P

Plate 7.17, Figs. 4–6; Plate 10.24, Figs. 1–3; Plate 11.11, Figs. 1–3; Plate 11.41, Figs. 7–9.

Pollen, monad, shape spheroidal, outline circular, diameter 16–19 μm under SEM and 15–22 μm under LM, pantoporate, 12–16 pori, tectate, columellate, pollen wall 1–1.3 μm (LM) thick, sculpture microechinate, perforate, 30–80 microechinae per 50 $\mu m^2$, aperture membrane densely covered with microechinae (SEM).

*Occurrence*: 9–0.8 Ma sedimentary rock formations at Hrútagil (9–8 Ma), Tjörnes (Reká, 4.2–4.0 Ma), Bakkabrúnir (1.7 Ma) and Svínafell (0.8 Ma).

### *Trollius* sp. P

Plate 11.11, Figs. 4–6.

Pollen, monad, shape subprolate, outline elliptic in equatorial view, polar axis 22 μm, equatorial diameter 16 μm under SEM, 26 μm and 22 μm under LM, tricolpate, colpi 17–18 μm long (SEM), 17 μm (LM), eutectate, columellate, pollen wall 1.2–1.3 μm thick (LM); sculpture striate, striae long, parallel, changing orientation across pollen surface; colpus membrane densely covered with microechinae.

*Occurrence*: 1.7 Ma sedimentary rock formation at Bakkabrúnir.

*Remarks*: Pollen grains from Iceland are very similar to extant material described by Lee and Blackmore (1992).

**Ranunculaceae gen. et spec. indet. 1** **P**

Plate 6.34, Figs. 1–3.

Pollen, monad, shape spheroidal to oblate, outline subcircular in polar view, equatorial axis 31–33 μm under SEM, 35–39 μm under LM, tricolpate, eutectate, columellate, pollen wall 1.5–2.3 μm thick (LM), sculpture perforate, microechinate, 0.4–0.5 μm in diameter, 35 microechinae per 50 $\mu m^2$ (SEM).

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

**Ranunculaceae gen. et spec. indet. 2** **P**

Plate 6.34, Figs. 4–9; Plate 7.17, Figs. 7–12; Plate 9.15, Figs. 4–9.

Pollen, monad, shape prolate, outline circular in polar view, subcircular or elliptic in equatorial view, polar axis 16–31 μm, equatorial diameter 11–26 μm under SEM, 21–34 μm and 13–29 μm under LM, tricolpate, colpi 13–24 μm long (SEM), 18–29 μm (LM); pollen eutectate, columellate, pollen wall 0.8–1.5 μm thick (LM), sculpture perforate, microechinate; 25–40 microechinae per 50 $\mu m^2$; aperture membrane covered with microechinae (SEM).

*Occurrence*: 10–1.1 Ma sedimentary rock formations at Tröllatunga (10 Ma), Hrútagil (9–8 Ma), Selárgil (5.5 Ma), Tjörnes (Egilsgjóta, Reká, Skeifá; 4.3–3.8 Ma), Bakkabrúnir (1.7 Ma) and Stöð (1.1 Ma).

*Remarks*: This morphotype may include more than one biological species.

**Ranunculaceae gen. et spec. indet. 3** **P**

Plate 9.15, Figs. 10–12.

Pollen, monad, shape subprolate, outline subcircular to lobate in polar view, elliptic in equatorial view; polar axis 16–20 μm, equatorial axis 12–18 μm under SEM, 17–23 μm and 12–22 μm under LM, tricolpate, eutectate, columellate, pollen wall 1.2–1.3 μm thick (LM), sculpture perforate, microechinate, ca 55 microechinae per 50 $\mu m^2$ (SEM).

*Occurrence*: 5.5–3.8 Ma sedimentary rock formations at Selárgil (5.5 Ma) and Tjörnes (4.3–3.8 Ma).

**Ranunculaceae gen. et spec. indet. 4** **P**

Plate 10.25, Figs. 1–3.

Pollen, monad, shape prolate to spheroidal, outline lobate in polar view, elliptic in equatorial view; polar axis 18 μm, equatorial diameter 12–18 μm under SEM, 20 μm and 14–20 μm under LM, tricolpate, colpi 12–13 μm long (SEM), ca 16 μm

(LM); eutectate, columellate, pollen wall 1.5 μm thick (LM), sculpture microechinate, perforations indistinct, 130–150 microechinae per 50 μm$^2$ (SEM).

*Occurrence*: 4.3–4.2 Ma sedimentary formation at Tjörnes (Egilsgjóta).

**Ranunculaceae gen. et spec. indet. 5** **P**

Plate 10.25, Figs. 4–6.

Pollen, monad, shape subprolate, outline lobate in polar view, elliptic in equatorial view; polar axis 18–27 μm, equatorial diameter 14–26 μm under SEM, 23–31 μm and 19–32 μm under LM, tricolpate, colpi 13–15 μm long (SEM), 17–24 μm (LM); eutectate, columellate, pollen wall 1.3–1.5 μm thick (LM), sculpture perforate, microechinate, 52–85 microechinae per 50 μm$^2$ (SEM).

*Occurrence*: 4.3–4.0 Ma sedimentary rock formations at Tjörnes (Egilsgjóta, Reká).

**Ranunculaceae gen. et spec. indet. 6** **P**

Plate 11.11, Figs. 10–12.

Pollen, monad, shape prolate, outline lobate in polar view, elliptic in equatorial view; polar axis 17–18 μm, equatorial diameter 12–19 μm under SEM, 18 μm and 12–20 μm under LM, tricolpate, colpi 13–15 μm (SEM), 14 μm (LM); eutectate, columellate, pollen wall 0.7–0.8 μm thick (LM), sculpture perforate; perforations inconspicuous, microechinate, 40–60 microechinae per 50 μm$^2$ (SEM).

*Occurrence*: 1.7 Ma sedimentary rock formation at Bakkabrúnir.

**Ranunculaceae gen. et spec. indet. 7** **P**

Plate 11.44, Figs. 1–3.

Pollen, monad, shape spheroidal, outline circular; diameter 15–18 μm under SEM, 18–19 μm under LM, pantocolpate, ≤ 9 colpi; colpi 5–7 μm long (SEM); eutectate, columellate, pollen wall 1.6 μm thick (LM), sculpture rugulate-verrucate, perforate, microechinate, aperture membrane covered with blunt microechinae (SEM).

*Occurrence*: 0.8 Ma sedimentary rock formation at Svínafell.

**Rosaceae**

***Alchemilla* sp.** **M**

Plate 11.43, Figs. 2–4.

Leaves, petiolate; petiole rarely preserved, >3 mm long, lamina symmetrical, oblate, 2.0–2.5 cm long, 3–3.5 cm wide, length to width ratio 0.6–0.8, apex acute to obtuse, base auriculate, margin lobed; lobes 6.2–8.8 mm wide, 4.9–5.1 mm long,

serrate, 13 teeth per lobe, teeth regularly spaced, simple, served by primary, secondary or branches of secondary veins, basal side convex or acuminate, apical side straight, concave or acuminate, primary venation actinodromous, seven primary veins, in some cases lowest pair of primary veins thinner than remaining primaries, the innermost lateral veins arising at angles of 30–40° from central vein, following pair of primary veins arising at angles of 56–84° from central vein, outermost pair of primary veins arising at angles of 120–124° from central vein, secondary venation craspedodromous to semicraspedodromous, five to six pairs of secondary veins per lobe segment, diverging from primary veins at angles of 22–25°, alternate and curving upwards, tertiary venation orthogonal reticulate, quaternary veins forming areoles of variable shape and size with tertiary veins, ultimate veins simple, branching or branched twice.

*Occurrence*: 0.8 Ma sedimentary rock formation at Svínafell.

**cf. *Crataegus* sp.** **M**

Plate 8.12B, Figs. 6, 7.

2005 cf. *Crataegus* sp. – Denk et al.: p. 395, figs. 142–143.

One, probably apical, leaf fragment, margin coarsely dentate; each tooth with a small subsidiary tooth on the basal side.

*Occurrence*: 7–6 Ma sedimentary formation at Fífudalur.

***Crataegus* sp.** **P**

Plate 10.37, Figs. 10–12.

Pollen, monad, shape subprolate, elliptic in equatorial view; polar axis ca 27 μm, equatorial diameter ca 23 μm under SEM, polar axis and equatorial diameter ca 29 under LM, tricolporate, colpi ca 23 μm long (SEM), tectate, columellate, pollen wall ca 1.4 μm thick (LM), sculpture striate; striation dense, 2–6 μm long and 0.2–0.4 μm wide, striae merging at regular intervals and forming knob-like protrusions (SEM).

*Occurrence*: 10 Ma sedimentary formation at Tröllatunga.

***Dryas octopetala* L.** **M**

Plate 11.7, Fig. 4; Plate 11.43, Fig. 5.

1978 *Dryas octopetala* L. *fossilis* – Akhmetiev et al.: pl. 14, figs. 1, 3, 7, 9, 13; pl. 16, figs. 11, 25.

Leaves, lacking a preserved petiole, lamina lobed, 7.5–8 mm long, 5.5–6.5 mm wide, length to width ratio 1.2–1.4, lamina symmetrical, wide ovate, base cordate, apex obtuse to bluntly acute, margin crenate, secondary venation craspedodromous, five pairs of secondary veins, departing from primary vein at wide angles in basal

part and narrower angles in apical parts, secondary veins straight to slightly curved ending in tooth apex.

*Occurrence*: 2.4–0.8 Ma sedimentary rock formations at Gljúfurdalur (2.4–2.1 Ma), Bakkabrúnir (1.7 Ma), Stöð (1.1 Ma) and Svínafell (0.8 Ma).

***Filipendula* sp.** **P**

Plate 10.25, Figs. 7–9.

Pollen, monad, shape subprolate to spheroidal, outline circular in equatorial view, polar axis 17–18 μm, equatorial diameter 14–17 under SEM, 19–22 μm and 13–22 μm under LM, tricolporate, colpi 9–12 μm long (SEM), 13–17 μm (LM); tectate, columellate, pollen wall 1.3 μm thick (LM), sculpture microechinate, perforate; perforations barely visible; tectum arching over porus forming a short "bridge" (SEM).

*Occurrence*: 4.3–3.8 Ma sedimentary rock formations at Tjörnes (Egilsgjóta, Reká, Skeifá).

***Fragaria* sp.** **P**

Plate 10.25, Figs. 10–12; Plate 11.12, Figs. 1–6.

Pollen, monad, shape prolate, outline lobate in polar view, elliptic in equatorial view, polar axis 17–27 μm, equatorial diameter 9–20 μm under SEM, 20–32 μm and 11–25 μm under LM, tricolporate, colpi 13–21 μm long (SEM), 16–25 μm (LM); tectate, columellate, pollen wall 1–1.3 μm thick (LM), sculpture striate, striae long, ridges of striae sharply crested and separated by relatively narrow grooves, surface between ridges perforate; perforations barely visible, tectum arching over aperture zone, partly covering operculum; operculum elliptic (SEM).

*Occurrence*: 4.3–1.7 Ma sedimentary rock formations at Tjörnes (Egilsgjóta, Reká, Skeifá; 4.3–3.8 Ma) and Bakkabrúnir (1.7 Ma).

*Remarks*: Unlike pollen of *Geum* and *Potentilla*, grooves between the striae are not distinctly perforate in *Fragaria*. Contrary to *Fragaria* and *Potentilla*, *Geum* has no operculum. The fossil pollen is similar to the extant *F. virginiana* Duchesne (Hebda et al. 1988) and *F. moschata* (Duchesne) Duchesne (Halbritter 2005).

***Potentilla* sp.** **M**

Plate 11.26, Figs. 1–2.

Leaf, odd pinnately compound, 1.6 cm long, 1.4 cm wide, three pairs of lateral leaflets, one terminal leaflet, leaflets opposite, leaflet lamina elliptic, coarsely serrate, three teeth on each side plus a terminal tooth, basal and apical side of teeth convex, secondary venation craspedodromous.

*Occurrence*: 1.1 Ma sedimentary rock formation at Stöð.

***Potentilla* sp. 1** **P**

Plate 10.27, Figs. 10–12.

Pollen, monad, shape subprolate, outline lobate in polar view, elliptic in equatorial view; polar axis ca 18 μm, equatorial diameter ca 22 μm under SEM, ca 29 μm and 30 μm under LM, tricolporate, tectate, columellate, pollen wall ca 1.5 μm thick (LM), sculpture striate; striae slightly crested, striae 0.5–1 μm wide and up to 9.5 μm long, wide grooves between striae, grooves perforate (SEM).

*Occurrence*: 4.3–4.2 Ma sedimentary rock formation at Tjörnes (Egilsgjóta).

***Potentilla* sp. 2** **P**

Plate 11.26, Figs. 3–5.
Pollen, monad, shape prolate, outline lobate in polar view, elliptic in equatorial view, polar axis ca 17 μm, equatorial diameter ca 11 μm under SEM, ca 20 μm and 13 μm under LM, tricolporate, colpi ca 14 μm long (SEM), 15–16 μm (LM); tectate, columellate, pollen wall ca 1.2 μm thick (LM), sculpture striate; striae long, ridges of striae crested and separated by relatively wide grooves, surface between ridges densely perforate, tectum arching over aperture zone, partly covering operculum (SEM).

*Occurrence*: 1.1 Ma sedimentary rock formation at Stöð.

***Rubus* sp.** **P**

Plate 10.27, Figs. 1–3.

Pollen, monad, shape prolate, outline lobate in polar view, elliptic in equatorial view, polar axis 18–24 μm, equatorial diameter 12–16 μm under SEM, 21–27 μm and 18–19 μm under LM, tricolporate, colpi 14–19 μm long (SEM), 13–20 μm (LM); tectate, columellate, pollen wall 1.6–1.8 μm thick (LM), sculpture striate, striae wide, forming a "braided" pattern, ridges of striae slightly crested and separated by narrow grooves, surface between ridges perforate, perforations barely visible, tectum arching over aperture zone (SEM).

*Occurrence*: 4.2–4.0 Ma sedimentary rock formation at Tjörnes (Reká).

***Sanguisorba* sp.** **P**

Plate 4.15, Figs. 1–3; Plate 5.18, Figs. 7–12; Plate 6.38, Figs. 7–12; Plate 9.16, Figs. 1–6; Plate 10.27, Figs. 4–6; Plate 11.12, Figs. 7–9.

Pollen, monad, shape subprolate, outline circular to convex triangular in polar view, polar axis 16–33 μm, equatorial diameter 16–30 under SEM, 20–41 μm and 19–35 μm under LM, tricolporate, colpi 12–23 μm long (SEM), 14–23 μm (LM); tectate, columellate, pollen wall 1.1–1.7 μm thick (LM), sculpture weakly striate,

perforate, colpi and pori area entirely covered with an operculum, operculum with microechinae and perforations (SEM).

*Occurrence*: 15–1.7 Ma sedimentary rock formations at Botn (15 Ma), Surtarbrandsgil (12 Ma), Tröllatunga, Húsavíkurkleif (10 Ma), Selárgil (5.5 Ma), Tjörnes (Egilsgjóta, Reká, Skeifá; 4.3–3.8 Ma) and Bakkabrúnir (1.7 Ma).

**aff. *Sorbus* sp. (‘*S. aria* type’)** **M**

Plate 8.12A, Figs. 1–3

Leaves, petiolate; petiole up to 1.8 cm long, lamina elliptic, slightly asymmetrical, 4.8–5.8 cm long, 2.4–3.2 cm wide, length to width ratio 1.8–2, base acute, apex acuminate, 13 pairs of secondary veins, rather densely spaced, originating from primary vein at intervals of 3–6 mm, departing from primary vein at angles of 55–25°, course of secondary veins straight, secondary venation craspedodromous, terminal branches of secondary veins running into secondary teeth, margin serrate above basal area, 1–3 small and sharp secondary teeth

*Occurrence*: 7–6 Ma sedimentary rock formation at Brekkuá.

***Sorbus* aff. *aucuparia*** **M**

Plate 10.23, Figs. 3–6; Plate 11.43, Fig. 6.

1963 *Sorbus* sp. – Thorarinsson: pl. 6, fig. 1.

Leaves, odd pinnately compound, estimated length 12–15 cm, 5–7 cm wide, petiole 2.3–2.6 cm long, stipules on proximal part of petiole; five pairs of leaflets preserved, attachment scars on rhachis suggest six to seven pairs of leaflets plus a terminal leaflet; leaflets decussate, 1.7–4.5 cm long, 7–20 mm wide, lamina symmetrical, narrow to wide elliptic, base slightly asymmetrical, leaflets narrow oblong, apex acute, base rounded, margin serrate, teeth simple or compound, apical side straight to acuminate, basal side convex to acuminate and longer, teeth served by secondary veins, branches of secondary veins or tertiary veins, petiolule short, 0.5–1.4 mm long, venation pinnate, secondary venation semicraspedodromous to craspedodromous, 7–12 pairs of secondary veins.

*Occurrence*: 3.9–0.8 Ma sedimentary rock formations at Tjörnes (Skeifá, 3.9–3.8 Ma) and Svínafell (0.8 Ma).

*Remarks*: The leaflets included within this taxon are quite variable. Based on our own observations of living populations, leaflets are highly polymorphic in texture, size, shape, and dentition. Coriaceous leaves with reduced or absent dentition are more typical of exposed trees, whereas large chartaceous leaves with simple or double serrate leaves are typical of forests.

**Rosaceae gen. et spec. indet., type A (? Prunoideae)** **M**

Plate 5.17, Figs. 1–3, 7; Plate 6.35, Figs. 1–2; Plate 8.12A, Figs. 4–5.

1966 *Ulmus*? sp. – Friedrich: p. 77, pl. 2, fig. 3.
2005 Rosaceae gen. et spec. indet., type A (? Prunoideae) – Denk et al.: p. 395, figs. 127–136.

Leaves petiolate; one specimen with 1.6 cm long petiole preserved, lamina ovate or elliptic, serrate, 6–12 cm long, 3.5–6 cm wide, base rounded, symmetrical, apex (elongate) acute, secondary venation brochidodromous to craspedodromous (apically), from the loops small veins supplying teeth; teeth triangular with basal side slightly longer or as long as apical side, both sides ± convex, gland-like dark spots in sinuses between two teeth, locally teeth with glandular tip, rarely very small subsidiary teeth present.

*Occurrence*: 12–6 Ma sedimentary rock formations at Seljá, Surtarbrandsgil (12 Ma), Tröllatunga (10 Ma) and Brekkuá (7–6 Ma).

*Remarks*: Leaves from the Middle Miocene of North America displaying very similar tooth architecture have been assigned to *Amelanchier* Medik. (Schorn and Gooch 1994). They differ from the Icelandic leaves by their entire margin in the basal part of the leaf. There are, however, also species of *Amelanchier* with teeth along the whole margin, such as *Amelanchier asiatica* Endl. ex Walp. Moreover, similar leaves from the Neogene of Central Europe have been ascribed to *Cerasus* (Adans.) Focke (= *Prunus* L.) by Knobloch (1998). We tentatively assign the Icelandic leaves to Prunoideae within the Rosaceae, because of their overall similarity with *Prunus*.

**Rosaceae gen. et spec. indet., type B (? Prunoideae)** **M**

Plate 5.17, Fig. 4, 8.

2005 Rosaceae gen. et spec. indet., type B (? Prunoideae) – Denk et al.: p. 395, figs. 137–139.

Leaves, no petiole preserved, lamina elliptic, serrate, ca 9 cm long, 4 cm wide, base slightly cordate, apex acute (acuminate), secondary venation brochidodromous, venation pattern close to the margin not preserved, teeth triangular with basal side slightly longer than apical side.

*Occurrence*: 12 Ma sedimentary formation at Surtarbrandsgil.

*Remarks*: The few leaves resemble *Prunus* in their shape, size and dentition.

**Rosaceae gen. et spec. indet., type C** **M**

Plate 5.17, Figs. 5–6.

2005 Rosaceae gen. et spec. indet., type C – Denk et al.: p. 395, figs. 140–141.

Leaf, petiole not preserved, lamina elliptic, serrate, >7.3 cm long, 2.9 cm wide, base acute, apex acute, secondary venation brochidodromous, secondary veins branching close to the margin, one branch running to the subsequent secondary vein (forming a loop) the other branch curving towards the apex and sending two further small branches into the tooth and the sinus between adjacent teeth.

*Occurrence*: 12 Ma sedimentary formation at Surtarbrandsgil.

*Remarks*: Partly similar leaves have been ascribed to *Sorbus* cf. *uzenensis* Huzioka by Knobloch (1998). We tentatively assigned this leaf to Rosaceae. We cannot exclude that it belongs to the same type of plant as do the leaves assigned to Rosaceae gen. et spec. indet. Type B (? Prunoideae) described above.

**cf. Rosaceae** **M**

Plate 5.17, Fig. 9.

A small fruit, 9 mm in diameter, with the remnants of the calyx preserved.

*Occurrence*: 12 Ma sedimentary rock formation at Seljá.

**Rosaceae gen. et spec. indet. 1** **P**

Plate 4.15, Figs. 4–6.

Pollen, monad, shape subprolate to spheroidal, outline elliptic to circular in equatorial and polar view, polar axis ca 27 μm, equatorial diameter ca 23 μm under SEM, ca 31 μm and ca 28 μm under LM, tricolporate, colpi ca 20 μm long (SEM), eutectate, columellate, sculpture striate; striae not oriented, short, 1.3–5.1 μm long, 0.2–0.5 μm wide, merging to form a glabrous tectum close to aperture; mesocolpium arching over porus (SEM).

*Occurrence*: 15 Ma sedimentary rock formation at Botn.

**Rosaceae gen. et spec. indet. 2** **P**

Plate 4.15, Figs. 7–9.

Pollen, monad, shape prolate to spheroidal, outline elliptic in equatorial view, polar axis ca 20 μm, equatorial diameter ca 16 μm under SEM, ca 24 μm and 19 μm under LM, tricolporate, colpi 16–17 μm long (SEM), 18–20 μm (LM), tectate, columellate, pollen wall 0.8 μm thick (LM), sculpture striate; striae parallel to polar axis, intertwining, 2.1 to >7 μm long, 0.2–0.3 μm wide; striate tectum arching over porus (SEM).

*Occurrence*: 15 Ma sedimentary rock formation at Botn.

**Rosaceae gen. et spec. indet. 3 (*Prunus*)** **P**

Plate 4.15, Figs. 10–12; Plate 5.18, Figs. 1–6; Plate 6.35, Figs. 7–12.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis 22–31 μm, equatorial diameter 16–29 μm under SEM, 22–37 μm and 22–32 μm under LM, tricolporate, colpi 21–26 μm long (SEM), 26–31 μm (LM), tectate, columellate, pollen wall 1.0–1.6 μm thick (LM), sculpture striate; striae parallel to polar axis, arranged in a single plane, individual striae 1.3–6.6 μm long, 0.2–0.5 μm wide (width of striae varies between grains), tectum arching over porus from both sides (SEM).

*Occurrence*: 15–10 Ma sedimentary rock formations at Botn (15 Ma), Surtarbrandsgil (12 Ma), Tröllatunga and Húsavíkurkleif (10 Ma).

**Rosaceae gen. et spec. indet. 4** **P**

Plate 6.36, Figs. 1–3.

Pollen, monad, shape subprolate to spheroidal, outline elliptic in equatorial view, subcircular in polar view, polar axis ca 27 μm, equatorial diameter 21–24 μm under SEM, ca 31 μm and 28–30 μm under LM, tricolporate, colpi ca 24 μm long (LM), 18 μm (SEM), eutectate, columellate, pollen wall 1.6–2 μm thick (LM), sculpture striate; striae oriented parallel to polar axis in mesocolpium, perpendicular in aperture region, 0.9–6 μm long in mesocolpium and polar region, 0.6–2.4 μm in aperture region, wider in polar and aperture region, closely spaced; mesocolpium arching over porus (SEM).

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

**Rosaceae gen. et spec. indet. 5** **P**

Plate 6.36, Figs. 4–7.

Pollen, monad, shape subprolate to spheroidal, outline subcircular in equatorial view, circular in polar view, polar axis ca 16 μm, equatorial diameter ca 14 μm under SEM, 17 μm and 19 μm under LM, tricolporate, colpi ca 13 μm long (LM), 11 μm (SEM), eutectate, columellate, pollen wall ca 1.2 μm thick (LM), sculpture microrugulate-perforate, sexine (bridge) arching over porus (SEM).

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

**Rosaceae gen. et spec. indet. 6** **P**

Plate 6.36, Figs. 8–11.

Pollen, monad, shape subprolate to spheroidal, polar axis ca 24 μm, equatorial diameter ca 17 μm under SEM, ca 23 μm and 23 μm under LM, tricolporate, colpi ca

20 µm long (LM), eutectate, columellate, pollen wall ca 1.2 µm thick (LM), sculpture striate; striae forming sharp ridges, sexine (bridge) arching over porus (SEM).

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

**Rosaceae gen. et spec. indet. 7 (*Rubus*)** **P**

Plate 6.36, Figs. 12–14.

Pollen, monad, shape subprolate, outline elliptic in equatorial view, polar axis ca 23 µm, equatorial diameter ca 19 µm under SEM, ca 26 µm and 23 µm under LM, tricolporate, colpi ca 19 µm long (SEM), 18–20 µm (LM), eutectate, columellate, pollen wall ca 1.7 µm thick (LM), sculpture shallowly striate; striae partly fused and separated by narrow grooves; sexine arching over porus (SEM).

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

**Rosaceae gen. et spec. indet. 8** **P**

Plate 6.38, Figs. 1–3.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis ca 23 µm, equatorial diameter ca 17 µm under SEM, ca 23 µm and 19 µm under LM, tricolporate, colpi ca 19 µm long (SEM), ca 20 µm (LM), eutectate, columellate, pollen wall ca 1.4 µm thick (LM), sculpture shortly striate; striae 0.6–2.2 µm long, oriented parallel to polar axis.

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

**Rosaceae gen. et spec. indet. 9 (*Pyrus* sp.)** **P**

Plate 6.38, Figs. 4–6.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis ca 21 µm, equatorial diameter ca 13 µm under SEM, ca 22 µm and 13 µm under LM, tricolporate, colpi ca 17 µm long (SEM), eutectate, columellate, pollen wall ca 0.6 µm thick (LM), sculpture striate-perforate, striae sinuous, some ending in a sharp tip.

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

**Rosaceae gen. et spec. indet. 10** **P**

Plate 9.16, Figs. 7–12.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis 18–21 µm, equatorial diameter 12–13 µm under SEM, 18–22 µm and 13–14 µm

under LM, tricolporate, colpi 15–16 μm long (SEM), ca 15 μm (LM), tectate, columellate, pollen wall 0.8–1.3 μm thick (LM), sculpture striate, length of individual striae 0.7–5 μm, width of striae 0.2–0.3 μm, sexine slightly arching over porus from both sides (bridge), course of striae following arches (SEM).

*Occurrence*: 5.5 Ma sedimentary rock formation at Selárgil.

**Rosaceae gen. et spec. indet. 11** **P**

Plate 9.17, Figs. 1–3; Plate 10.27, Figs. 7–9.

Pollen, monad, shape prolate, outline lobate in polar view, elliptic in equatorial view; polar axis 23–25 μm, equatorial diameter 15–16 μm under SEM, 26–27 μm and 17–18 μm under LM, tricolporate, colpi 16–20 μm long (SEM), ca 20 μm (LM), tectate, columellate, pollen wall 1–1.2 μm thick (LM), surface sculpture striate; striae long, 0.4–0.6 μm wide, mostly oriented parallel to polar axis, occasionally striae oblique to main direction of striation (SEM).

*Occurrence*: 5.5–3.8 Ma sedimentary rock formations at Selárgil (5.5 Ma) and Tjörnes (Skeifá, 3.9–3.8 Ma).

**Rosaceae gen. et spec. indet. 12** **P**

Plate 9.17, Figs. 4–6.

Pollen, monad, shape prolate, outline elliptic in equatorial view; polar axis ca 21 μm, equatorial diameter ca 15 μm under SEM, ca 22 μm and 15 μm under LM, tricolporate, colpi 17 μm long (SEM), ca 17 μm (LM), tectate, columellate, pollen wall ca 1 μm thick (LM), sculpture striate; striae mostly parallel to polar axis, striae long, 0.15–0.2 μm wide, striae seperated by deep narrow grooves (SEM).

*Occurrence*: 5.5 Ma sedimentary rock formation at Selárgil.

**Rosaceae gen. et spec. indet. 13** **P**

Plate 11.12, Figs. 10–12.

Pollen, monad, shape prolate, outline lobate in polar view, elliptic in equatorial view; polar axis ca 23 μm, equatorial diameter ca 16 μm under SEM, ca 24 μm and 16 μm under LM, tricolporate, colpi 18–19 μm long (SEM), 22–23 μm (LM); tectate, columellate, pollen wall ca 0.8 μm thick (LM), sculpture striate, striae short (1–3.5 μm long), spindle-shaped, arranged in a braided pattern, striae with marked ridges; perforations on areas between ridges barely discernible; sexine (bridge) arching over porus (SEM).

*Occurrence*: 1.7 Ma sedimentary rock formation at Bakkabrúnir.

## Rubiaceae

### *Galium* sp. P

Plate 11.44, Figs. 4–6.

Pollen, monad, shape prolate, outline lobate in polar view, elliptic in equatorial view, polar axis ca 11 μm, equatorial diameter ca 9 μm under SEM, ca 13 μm and 12 μm under LM, hexacolpate, colpi 7.7–8.3 μm long (SEM), 8.3–8.5 μm (LM); tectate, columellate, pollen wall 1.3 μm thick (LM), sculpture perforate, microechinate (SEM).

*Occurrence*: 0.8 Ma sedimentary rock formation at Svínafell.

## Salicaceae

### *Populus* sp. A (ex group *Populus tremula* L.) M

Plate 5.19, Figs. 1–2.

1966 *Populus latior* Al. Braun cf. forma *transversa* Heer – Friedrich: p. 65, text-fig. 15.
2005 *Populus* sp. 1 (ex group *Populus tremula* L.) – Denk et al.: p. 395, figs. 144–148.

Leaves petiolate; petiole 4–6 cm long, lamina roundish, 8.3–12.8 cm long and 6–12 cm wide, length to width ratio 0.9–1.1, base slightly cordate, apex round, dentate along whole margin, teeth broad triangular, apex blunt, glandular, apical side short convex, basal side long, teeth of variable size and irregularly spaced, sinus between teeth concave, deep and wide, secondary venation brochidodromous to eucamptodromous, four to five pairs of secondary veins curved towards the apex, diverging from primary vein at angles of 69–33°, the basalmost pair with several abmedial branches, these forming loops from which smaller veins supply teeth, opadial vein running parallel to basal margin of lamina.

*Occurrence*: 12 Ma sedimentary rock formation at Seljá and Surtarbrandsgil.

*Remarks*: These leaves are distinct from another common European Neogene *Populus*, *P. populina* (Brongn.) Knobloch, by their more pronounced pinnate venation. They differ from leaves of the Miocene of Sornica, which Goeppert (1855) figured as *P. balsamoides* Goepp. and *P. emarginata* Goepp. by their smaller number of lateral veins. Furthermore, the leaves from Iceland differ from leaves from Öhningen described as *P. latior* A. Braun by Heer (1856) in their smaller length to width ratio and the dentate margin at the leaf base. They belong, however, to the section *Populus*, where they can be compared with the modern North American *P. tremuloides* Michx. and the European *P. tremula* L. Both these modern forma have similar variation in the size and density of dentition.

***Populus* sp. B** **M**

Plate 8.13, Fig. 1.

2005 *Populus* sp. 2 – Denk et al.: p. 399, figs. 149–150.

Leaves, lamina >6.7 cm long and >5 cm wide, the basal part missing, symmetrical, ?ovate, leaf apex acute to attenuate, margin incompletely preserved, finely crenulate to entire, venation pinnate, secondary venation camptodromous, secondary veins gradually diminishing towards apex, connecting to following secondaries by forming inconspicuous marginal loops, secondary veins alternate or opposite, diverging from the midvein at angles of 56–76° and originating at intervals of 4–8 mm in the middle part of the leaf, intersecondary veins originating from the primary midvein, 0–2 intersecondary veins between secondary veins, tertiary veins perpendicular or oblique to secondary veins, and usually forked, 5–6 tertiary veins per 1 cm secondary vein, marginal ultimate venation forming loops.

*Occurrence*: 7–6 Ma sedimentary rock formation at Hestabrekkur.

*Remarks*: The type of venation and margin, together with the shape of the leaves are typical of the genus *Populus*.

***Populus* sp. C** **M**

Plate 8.13, Figs. 2–3.

1978 *Populus* sp. 2 – Akhmetiev et al.: pl. 7, fig. 3.
2005 *Populus* sp. 3 – Denk et al.: p. 399, fig. 151.

Female catkin with several fruits; catkin approximately 6.4 cm long, capsules spirally arranged around a slender axis, axis ca 0.3–0.76 mm wide, capsules 4.5–5.1 mm long, 2.6–3.4 mm wide, length to width ratio 1.3–1.9, capsules wide to narrow obovate, slightly asymmetrical, subsessile with short but relatively stout petiole, distal region of capsules marked by a notch, capsules dehiscing by two or three valves.

*Occurrence*: 7–6 Ma sedimentary rock formation at Þrimilsdalur and Brekkuá.

*Remarks*: The form of the capsules and the way in which they are attached to the axis are characteristic of female *Populus* catkins. Akhmetiev et al. (1978) reported a similar specimen that most likely belongs to the same species.

***Salix gruberi* Denk, Grímsson and Z. Kvaček** **M**

Plate 5.19, Figs. 3–6; Plate 6.39, Fig. 1; Plate 7.18, Fig. 1; Plate 8.13, Figs. 4–6; Plate 9.18, Figs. 1–2, 5–6; Plate 10.26, Figs. 1–3.

1868 *Salix macrophylla* Heer – Heer: p. 146, pl. 25, fig. 3a, b.
1886 *Salix macrophylla* Heer – Windisch: p. 34.
1886 *Salix varians* Goepp. – Windisch: p. 33.
1966 *Salix tenera* A. Braun – Friedrich: 66, pl. 1, figs. 3, 12, text-fig. 16.
1975 *Salix* – Sigurðsson: fig. 4.

*Salix* sp. – Akhmetiev et al.: pl. 5, figs. 3, 6, 7, pl. 11, figs. 6, 13, 18, 19.
1978 *Salix* cf. *glauca* L. – Akhmetiev et al.: pl. 8, figs. 2, 9.
2005 *Salix gruberi* Denk, Grímsson and Z. Kvaček – Denk et al.: p. 400, figs. 152–162.

Leaves and fruitlets; leaves petiolate; petiole rarely preserved, 1.8 cm long, dilated at proximal end, lamina elliptic, 4–18 cm long, 3–5 cm wide, length to width ratio 2.6–3.8, entire or crenulate close to the leaf base and typically dentate towards the apex, dentition commonly inconspicuous, base rounded to acute, apex bluntly acute, 12 to >17 pairs of secondary veins, secondary venation eucamptodromous to brochidodromous, curved towards the apex and running almost parallel to the margin, secondary veins irregularly spaced, intersecondaries and/or tertiary veins typically running perpendicular to primary vein, small veins originating from secondaries supplying teeth, teeth appressed, reduced to glandular tips, basal side much longer than apical side; cuticles smooth, adaxial with solitary simple trichome bases, abaxial densely hairy on veins, stomata visible as spindle-shaped traces of the guard cells.

Capsules >10 mm long, bottle-shaped with a narrow curved apical part, dehiscing by two recurved valves.

*Occurrence*: 12–3.8 Ma sedimentary rock formations at Surtarbrandsgil, Seljá (12 Ma), Gautshamar, Húsavíkurkleif (10 Ma), Hrútagil (9–8 Ma), Þrimilsdalur, Fífudalur, Hestabrekkur, Brekkuá and Vindfell (7–6 Ma), Selárgil (5.5 Ma) and Tjörnes (Skeifá, 3.9–3.8 Ma).

*Remarks*: The Iceland willow differs from the Central European *Salix varians* Goepp. (incl. *S. macrophylla* Heer) by its indistinctly toothed margin, widely spaced secondaries and fewer intersecondaries. Hantke (1954) in his revision of the Schrotzburg flora interpreted less distinctly dentate and entire leaf forms (including *S. tenera* A. Braun) as extreme forms of *S. lavateri* A. Braun, which is a narrow-leafed species that has nothing in common with the willow from Iceland. The preserved epidermal structure does not differ from *S. lavateri* in the type of the pubescence but a more detailed comparison is unreliable due to the poor state of preservation of the only compression from Surtarbrandsgil studied. Specimens similar to *S. gruberi* have also been described from the Late Miocene of Alaska as *S. kachemakensis* Wolfe (Wolfe 1966). Among modern species, the North American *S. scouleriana* Barr. and particularly the European *Salix caprea* L. are similar to the Miocene willow from Iceland. *Salix caprea* shows a comparable variability in leaf size and shape, and has a wavy margin with irregular, shallow, blunt-pointed teeth.

### *Salix* sp. A M

Plate 8.13, Figs. 8–10; Plate 9.18, Figs. 3–4.

Leaves, petiolate; petiole 3.5–8.5 mm long, lamina 3.5–8 cm long, 1.2–2 cm wide, length to width ratio 2.5–3.9, elliptic to narrow elliptic, primary vein slightly curved, stout, secondary venation eucamptodromous, 9–15 secondary veins curving towards apex, 0–1 intersecondary veins, margin entire or minutely crenulate.

*Occurrence*: 7–5.5 Ma sedimentary rock formations at Þrimilsdalur, Hestabrekkur, Brekkuá (7–6 Ma) and Selárgil (5.5 Ma).

*Remarks*: Based on the elliptic, entire-margined leaves, this taxon appears to be distinct from *Salix gruberi*.

### *Salix* sp. B (‘*S. arctica*’ type) M

Plate 10.26, Fig. 4; Plate 11.7, Figs. 5–9; Plate 11.27, Figs. 3–10; Plate 11.45, Figs. 1–8; Plate 11.46, Figs. 1–6.

1939 *Salix* sp. – Líndal: pl. 18, fig. 1.
1963 *Prunus padus*? – Thorarinsson: pl. 5, fig. 2.
1963 *Salix lanata*? – Thorarinsson: pl. 7, fig. 2.
1963 *Salix* sp – Thorarinsson: pl. 7, figs. 3–5.
1978 *Salix* sp. 2 – Akhmetiev et al.: pl. 13, fig. 6, 11, 14.
1978 *Salix glauca* L. foss. – Akhmetiev et al.: pl. 14, figs. 8, 10, 12 ; pl. 15, figs. 2, 9, 13, 14, 16, 22 ; pl. 16, figs. 1–3, 5, 9, 10, 23, 24.
1978 *Salix* sp. – Akhmetiev et al.: pl. 15, figs. 12, 19.
1978 *Salix phylicifolia* L. foss. – Akhmetiev et al.: pl. 16, fig. 6.

Leaves, petiolate, petiole 2–6 mm long, lamina symmetrical, base sporadically asymmetrical, narrow obovate, oblanceolate, narrow elliptic or elliptic, 1–8.3 cm long, 4.5–44 mm wide, length to width ratio 1.4–3.6, base acute, rarely obtuse, apex acute to obtuse, margin entire, in some cases slightly revolute, primary vein stout, secondary venation camptodromous to brochidodromous, 6–13 pairs of secondary veins departing from primary vein at wide to very narrow angles, course of secondary veins highly variable, changing from slightly curved and running directly towards leaf margin to running almost parallel to primary vein and converging in apical part of leaf, 0–1(−3) intersecondary veins, tertiary veins mostly perpendicular to secondary veins, simple or forked, 2–6 tertiaries per 5 mm secondary vein.

*Occurrence*: 3.9–0.8 Ma sedimentary rock formations at Tjörnes (Skeifá, 3.9–3.8 Ma), Bakkabrúnir (1.7 Ma), Stöð (1.1 Ma) and Svínafell (0.8 Ma).

*Remarks*: Potential modern analogues of this taxon are morphologically extremely variable showing substantial overlap in leaf morphology between species. Hence, the fossil taxon might include more than one biological species. Apart from the modern *S. arctica* Pall., *S. lanata* L. shows considerable morphological overlap with the fossils.

### *Salix herbacea* L. M

Plate 11.28, Figs. 1–2; Plate 11.46, Figs. 7–10.

Leaves, petiolate; lamina symmetrical, 7–16 mm long, 6–15 wide, length to width ratio 1–1.4, suborbiculate, orbiculate or oblate, base obtuse, apex obtuse or emarginate,

margin crenate to bluntly serrate, teeth small, with long basal side and very short apical side, teeth commonly confined to upper half of lamina, secondary venation camptodromous to brochidodromous, the majority of secondary veins originating below middle of lamina and curving upwards, secondaries forming primary loops that are followed by higher order loops, four to eight pairs of secondary veins, 0–2 intersecondary veins, tertiary veins forked, 4–6 per 5 mm of secondary vein, areoles formed by quaternary veins, quadrangular to hexagonal.

*Occurrence*: 1.1–0.8 Ma sedimentary rock formations at Stöð (1.1 Ma) and Svínafell (0.8 Ma).

### *Salix* sp. 1 **P**

Plate 4.16, Figs. 1–9.

Pollen, monad, occurring in groups up to >20, shape subspheroidal, outline elliptic in equatorial view, polar axis 17–20 µm, equatorial diameter 13–15 µm under SEM, 21–25 µm and 16–18 µm under LM, tricolporate, colpi 15–16 µm long (SEM), semitectate, columellate, sculpture reticulate, forming undulate polygonal muri with small lumina, size of lumina decreasing from mesocolpium to aperture region and fusing to form an ectexine rim (margo) next to the aperture membrane, lumen 0.3–1.4 × 0.2–0.8 µm across in mesocolpium, «1 µm close to colpi, muri 0.3–0.5 µm in diameter, lumen beset with free-standing columellae of variable size and shape, aperture membrane densely covered with granula (SEM).

*Occurrence*: 15 Ma sedimentary rock formation at Botn.

### *Salix* sp. 2 **P**

Plate 5.19, Figs. 7–10; Plate 6.39, Figs. 2–4; Plate 8.11, Figs. 4–6.

Pollen, monad, shape subprolate, outline elliptic in equatorial view, polar axis 26–30 µm, equatorial diameter 23–29 µm under SEM, 28–38 µm and 28–37 µm under LM, tricolporate, colpi 24 µm long (SEM), semitectate, columellate, pollen wall 1.5–1.7 µm thick, sculpture heterobrochate reticulate, muri undulate, standing on short columellae, columellae hemispherical in cross-section, polygonal lumina, size of lumina decreasing from mesocolpium towards the colpi, lumen 1.1–3.3 × 0.3–1.7 µm across in mesocolpium, «1 µm close to colpi, muri 0.4–0.5 µm in diameter, lumen beset with freestanding columellae, mostly short and rounded (SEM).

*Occurrence*: 12–6 Ma sedimentary rock formations at Surtarbrandsgil (12 Ma), Tröllatunga, Húsavíkurkleif (10 Ma) and Brekkuá (7–6 Ma).

***Salix* sp. 3** **P**

Plate 6.39, Figs. 5–13; Plate 11.44, Figs. 7–9.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis 18–27 μm, equatorial diameter 13–16 μm under SEM, 22–28 μm and 16–20 μm under LM, tricolporate, colpi 16–17 μm long (SEM), 15–20 μm (LM) long, semitectate, columellate, pollen wall 1.7–2.7 μm, sculpture heterobrochate reticulate, muri undulate, 0.2–0.6 μm wide, standing on high columellae, lumina polygonal, 1.3–2.3×0.7–1.3 μm in diameter, lumen beset with free-standing columellae (SEM).

*Occurrence*: 10–0.8 Ma sedimentary rock formations at Tröllatunga, Húsavíkurkleif (10 Ma) and Svínafell (0.8 Ma).

***Salix* sp. 4** **P**

Plate 9.17, Figs. 7–9.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis ca 20 μm, equatorial diameter ca 15 μm under SEM, ca 22 μm and 19 μm under LM, tricolporate, colpi ca 18 μm (LM) long, semitectate, columellate, pollen wall ca 0.7 μm, sculpture heterobrochate reticulate, muri undulate, thin crested muri, 0.2–0.3 μm wide, muri standing on short columellae, lumina polygonal, 0.4–1.4 μm in diameter, lumen beset with widely spaced short freestanding columellae (SEM).

*Occurrence*: 5.5 Ma sedimentary rock formation at Selárgil,

***Salix* sp. 5 (‘*Salix caprea*’ type)** **P**

Plate 9.17, Figs. 10–12; Plate 10.28, Figs. 1–6; Plate 11.13, Figs. 1–9; Plate 11.29, Figs. 1–3; Plate 11.44, Figs. 10–12.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis 15.4–24 μm, equatorial diameter 7–17 μm under SEM, 18–28 μm and 10–20 μm under LM, tricolporate, colpi 15–19 μm long (SEM), 18–23 μm (LM); semitectate, columellate, pollen wall 1–1.6 μm thick (LM), sculpture heterobrochate reticulate, muri undulate, muri high, standing on short columellae, triangular in cross-section, muri sometimes with small perforations (extremely small lumina), muri 0.4 μm in diameter, lumina 0.3–1.4 in diameter, lumina beset with free-standing columellae, size of lumina abruptly decreasing close to aperture, merging to form an ectexine rim (margo) along colpi; colpus membrane beset with polygonal elements, (SEM).

*Occurrence*: 5.5–0.8 Ma sedimentary rock formations at Selárgil (5.5 Ma), Tjörnes (Egilsgjóta, Reká; 4.3–4.0 Ma), Bakkabrúnir (1.7 Ma), Stöð (1.1 Ma) and Svínafell (0.8 Ma).

*Remarks*: The reticulum displays some variability ranging from narrow to very loose. This is likely to be within the range of variability found in a single species.

***Salix* sp. 6** **P**

Plate 11.13, Figs. 10–12.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis ca 21 μm, equatorial diameter ca 15 μm under SEM, ca 23 μm and 17 μm under LM, tricolporate, colpi ca 18 μm long (SEM), ca 18 μm (LM); semitectate, columellate, pollen wall ca 1.3 μm thick (LM), sculpture heterobrochate reticulate, lumina roundish, size of lumina decreasing towards aperture.

*Occurrence*: 1.7 Ma sedimentary rock formation at Bakkabrúnir.

***Salix* sp. 7** **P**

Plate 11.29, Figs. 4–6.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis ca 15 μm, equatorial diameter ca 11 μm under SEM, ca 17 μm and 13 μm under LM, tricolporate, colpi ca 10 μm long (SEM), ca 14 μm (LM); semitectate, columellate, pollen wall ca 1.3 μm thick (LM), sculpture heterobrochate reticulate, muri undulate, muri with rounded crests, size of lumina abruptly decreasing near aperture, lumina beset with densely spaced free-standing columellae (SEM).

*Occurrence*: 1.1 Ma sedimentary rock formation at Stöð.

***Salix* sp. 8 (‘*Salix arctica*’ type)** **P**

Plate 11.37, Figs. 1–6.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis 21–24 μm, equatorial diameter 12–14 μm under SEM, 18–24 μm and 12–13 μm under LM, tricolporate, colpi 18–21 μm long (SEM), 18–20 μm (LM); semitectate, columellate, pollen wall ca 1.3 μm thick (LM), sculpture heterobrochate reticulate, muri undulate, lumina polygonal, large in mesocolpium, size of lumina abruptly decreasing towards aperture (margo), muri standing on short columellae, muri hemispherical in cross-section, lumina beset with densely spaced free-standing columellae of different size.

*Occurrence*: 0.8 Ma sedimentary rock formation at Svínafell.

## Sapindaceae

### *Acer crenatifolium* Ettingshausen

**subsp. i*slandicum* Denk, Grímsson and Z. Kvaček** **M**

Plate 5.20, Figs. 3–7; Plate 6.40, Figs. 4–9; Plate 7–19, Figs. 1–3.

1859 *Vitis islandica* Heer – Heer: p. 319
1868 *Vitis islandica* Heer – Heer: p.150, pl. 26, figs. 1f, 7a.

1868 *Acer otopterix* Goepp. – Heer: p. 152, pl. 25, fig. 1a, pl. 28, figs. 1, 3, 4, 2, 5–8.
1886 *Acer crenatifolium* Ettingshausen – Windisch: p. 258.
1966 *Acer crenatifolium* Ettingshausen – Friedrich: p. 84, pl. 5, figs. 1–3.
1978 *Acer crenatifolium* Ettingshausen – Akhmetiev et al.: p. 177, 178, pl. 3, fig. 1, pl. 4, fig. 1b, pl. 5, figs. 4, 9, 10.
1981 *Acer* sp. – Friedrich and Símonarson: fig. 5.
1982 *Acer islandicum* Friedrich and Símonarson – Friedrich and Símonarson: p. 159, pl. 1, figs. 1–4, 6–8, pl. 2, figs. 1–6, pl. 3, figs. 5, 7, 8, pl. 4, figs. 1, 4, pl. 5, figs. 1–4.
1982 *Acer* sp. 1 – Friedrich and Símonarson: p. 162, pl. 3, fig. 1, figs. 3–6, 8, pl. 4, fig. 2.
1983 *Acer* sp. – Friedrich and Símonarson: fig. 6.
2005 *Acer crenatifolium* Ettingshausen subsp. *islandicum* Denk, Grímsson and Z. Kvaček – Denk et al.: p. 400, figs. 163–169.

Leaves and samaras.

Leaves petiolate; petiole not preserved in most cases, >2.2 cm long in one specimen, lamina variable in size, 3 to >15 cm long, 2 to >14 cm wide, palmate, three- to five-lobed, lobes serrate, leaf base cordate, apex acute, actinodromous, secondary veins craspedodromous, teeth rather coarse, regularly spaced, basal side slightly convex to straight, apical side straight to concave; obtained cuticle structure shows straight-walled polygonal cells of the adaxial epidermis and less distinct cells with anomocytic stomata of the abaxial epidermis, guard cells elliptic, with a large aperture, solitary simple trichomes on veinlets 180 μm long.

Samaras 2.0–3.5 cm long, pericarp 8–15 mm long, 5–8 mm wide, pericarp length to width ratio 1.2–1.6, elliptic, with a wide attachment scar, 5–7 mm wide, samaras forming angles of 30–80°, wings 1.3–2.7 cm long, 6.6–15 mm wide; peduncle >20 mm long.

*Occurrence*: 12–8 Ma sedimentary rock formations at Surtarbrandsgil (12 Ma), Húsavíkurkleif, Tröllatunga (10 Ma) and Hrútagil (9–8 Ma).

*Remarks*: This subspecies is closely related to *Acer crenatifolium* subsp. *crenatifolium*, and indistinguishable from this Central European maple by leaf epidermal features (see Friedrich and Símonarson 1982, and Denk et al. 2005 vs. Walther 1972). It is part of a group of maples that was widespread during the Cainozoic in the Northern Hemisphere and is comparable with the modern section *Rubra* Pax that shows a disjunction between East Asia and North America. Based on epidermal features, Walther (1972) found also similarities of *A. crenatifolium* to the modern *A. hyrcanum* Fisch. and C. A. Mey. from the Balkans and northern Iran. The fossil species *Acer tricuspidatum* Braun and Agassiz (Bronn 1838) differs in mostly densely hairy lower leaf surface and more quadrangular/elliptic shape of the guard cell pairs. As Walther (1972) stated, *A. tricuspidatum* matches in epidermal features *A. saccharinum* L. rather than *A. rubrum* L. Hence, we do not support the reduction of *A. crenatifolium* to a form of *A. tricuspidatum*, as proposed by Procházka and Bůžek (1975).

### *Acer askelssonii* Friedrich and Símonarson M

Plate 5.20, Figs. 1–2; Plate 6.40, Figs. 1–3; Plate 7.18, Figs. 2–3; Plate 8.14, Figs. 1–2; Plate 8.15, Figs. 1–5.

1868 *Platanus aceroides* Goepp. – Heer: p. 150, pl. 26, fig. 5.
1868 *Acer otopterix* Goepp. – Heer: p. 152, pl. 28, figs. 9–11, 12, 13.
1976 *Acer* sp. 2 – Friedrich and Símonarson: p. 163, pl. 6, figs. 1–3.
1978 *Acer* sp. ex sect. *Platanoidea* Pax – Akhmetiev et al.: pl. 10, figs. 3, 4.
1981 *Acer* sp. – Friedrich and Símonarson: fig. 6.
2005 *Acer askelssonii* Friedrich and Símonarson – Denk et al.: p. 403, figs. 170–173.
2005 *Acer askelssonii* Friedrich and Símonarson – Grímsson et al.: p. 22, fig. 5, a–b.
2005 *Acer* sp. aff. *askelssonii* Friedrich and Símonarson – Grímsson et al.: p. 24, fig. 5, c–d.

Leaves and samaras; leaves palmate, petiole rarely preserved, >5.5 cm in one specimen, lamina five- to seven-lobed, entire with one or two coarse teeth per lobe, 3–15 cm long, 3.5–18 cm wide, secondary venation craspedodromous or brochidodromous, leaf base cordate, apex attenuate, lobe apex attenuate, teeth triangular acute to acuminate.

Samaras 5–9 cm long, up to 2.4 cm wide, with large pericarp, 1.5–3.6 cm long, 0.8–2 cm wide, length to width ratio of pericarp 1.4–1.7, attachment scar 0.7–2 cm wide.

*Occurrence*: 12–6 Ma sedimentary rock formations at Surtarbrandsgil (12 Ma), Húsavíkurkleif, Tröllatunga (10 Ma), Hrútagil (9–8 Ma) and Brekkuá, Hestabrekkur and Þrimilsdalur (7–6 Ma).

*Remarks*: These leaf remains resemble the modern species *A. platanoides* L. and *A. saccharum* Marsh. Whilst *A. saccharum* is the only North American species of a group of closely related species from western Eurasia and North America including *A. hyrcanum* Fischer and C. A. Mey. and *A. opalus* Mill. among others (Tian et al. 2002; Grimm et al. 2007), *A. platanoides* belongs to a group of Eurasian species including *A. campestre* L. and *A. laetum* C. A. Mey. (syn. *A. cappadocicum* Gleditsch). The fossil leaves co-occur with large samaras in the Hreðavatn-Stafholt Formation that were described as *Acer askelssonii* by Friedrich and Símonarson (1976) and suggested to be most closely related to *A. saccharinum* among modern maples. The samaras of *A. askelssonii*, however, display a large zone of attachment of the two pericarps, which is not the case in *A. saccharinum* showing a reduced point-like attachment scar.

### *Acer* sp. 1 (section *Acer*?) P

Plate 4.17, Figs. 1–3; Plate 6.41, Figs. 1–3; Plate 7.20, Figs. 1–9; Plate 8.11, Figs. 7–12; Plate 10.28, Figs. 7–9.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis 26–34 μm, equatorial diameter 16–23 μm under SEM, 31–43 μm and 19–31. μm

under LM, tricolpate, colpi 20–27 μm long (SEM), 24–34 μm (LM), tectate, columellate, pollen wall 1.4–1.7 μm thick, sculpture striate, striae long and 0.2–0.4 μm wide, mostly parallel (SEM).

*Occurrence*: 15–3.8 Ma sedimentary rock formations at Botn (15 Ma), Surtarbrandsgil (12 Ma), Tröllatunga, Húsavíkurkleif (10 Ma), Hrútagil (9–8 Ma), Hestabrekkur (7–6 Ma) and Tjörnes (Egilsgjóta, Reká; 4.3–4.0 Ma).

*Remarks*: Pollen of modern *Acer* has been described and figured by Fürstl (2002) and Clarke and Jones (1978), among others.

### *Acer* sp. 2 P

Plate 4.17, Figs. 4–6; Plate 5.21, Figs. 7–9; Plate 7.20, Figs. 10–12; Plate 10.28, Figs. 10–12.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis 30–34 μm, equatorial diameter 20–23 μm under SEM, 35–41 μm and 25–27 μm under LM, tricolpate, colpi 26–28 μm long (SEM), 29–34 μm (LM), tectate, columellate, pollen wall ca 2 μm thick, sculpture striate, striae short, closely spaced mostly divergent, striae 0.6–5 μm long and 0.2–0.7 μm wide (SEM).

*Occurrence*: 15–3.8 Ma sedimentary rock formations at Botn (15 Ma), Surtarbrandsgil (12 Ma), Tröllatunga, Húsavíkurkleif (10 Ma), Hrútagil (9–8 Ma), Hestabrekkur (7–6 Ma) and Tjörnes (Reká, Skeifá; 4.2–3.8 Ma).

### *Acer* sp. 3 P

Plate 5.21, Figs. 1–6; Plate 6.41, Figs. 4–6.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis 20–26 μm, equatorial diameter 14–15 μm under SEM, 29–31 μm and ca 17 μm under LM, tricolpate, colpi 21–22 μm long (SEM), ca 25 μm (LM), tectate, columellate, pollen wall ca 0.9 μm thick, sculpture striate, striae separated by perforations and grooves, striae short to long and 0.2–0.4 μm wide (SEM).

*Occurrence*: 12–10 Ma sedimentary rock formations at Surtarbrandsgil (12 Ma) and Tröllatunga (10 Ma).

### *Acer* sp. 4 P

Plate 6.41, Figs. 7–13.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis 28–43 μm, equatorial diameter 16–33 μm under SEM, 28–45 μm and 23–32 μm under LM, tricolpate, colpi 23–36 μm long (SEM), 33–34 μm (LM), tectate, columellate, pollen wall 1.5–1.7 μm thick, sculpture striate, striae short and separated by perforations and grooves, striae branching radially or in series (SEM).

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

### *Aesculus* sp. M

Plate 4.17, Figs. 7–9.

1957 *Ostrya selárdaliana* Áskelsson – Áskelsson: p. 27, fig. 4.
1957 *Carya* sp. – Áskelsson: p. 28, fig. 5.
1978 ?*Ostrya selardariana* Áskelsson – Akhmetiev et al.: pl. 1, fig. 4.
2007a *Aesculus* sp. – Grímsson et al.: p. 201, pl. 11–13.
2007b *Aesculus* sp. – Grímsson et al.: fig. 5.

Leaflets petiolate; preserved part of petiole 4.5–10 mm long, lamina 7.0–19.6 cm long and 2.2–7.6 cm wide, length to width ratio 2.2–3.2, widest in middle part, elliptic to narrow elliptic, symmetrical; base acute to cuneate, symmetrical or asymmetrical; apex attenuate; margin serrate, tooth apex acute to obtuse, apical side of teeth straight to concave, short, basal side straight to convex, long, sinuses between teeth rounded, teeth regularly spaced, simple, showing slight variation in size; primary venation pinnate, midvein moderate to stout, straight to curved or slightly sinuous; secondary venation craspedodromous, in some cases semicraspedodromous; up to 26 pairs of secondary veins diverging from the midvein at moderate to narrow angles of 70–31°, veins commonly more acute on one side of the lamina, subopposite to alternate, sometimes irregularly spaced, originating at intervals of 3–13 mm, 6–13 secondary veins per 5 cm primary vein, secondary veins straight in proximal part, curved upwards close to margin, sending off branches that end in teeth, secondary veins locally forming loops and connecting to external vein of following secondary vein; secondary veins and their external branches ending in teeth, thickness of veins typically decreasing abruptly when approaching tooth; tertiary veins much thinner than secondary veins, sinuous and anastomosing with quaternary veins, pattern orthogonal reticulate, forming almost right angles with secondary veins; quaternary veins randomly oriented, anastomosing with tertiary veins; fifth ordered veins thin, forming areoles that are well-developed, randomly arranged, polygonal; small protrusions visible on lamina.

*Occurrence*: 15 Ma sedimentary rock formation at Selárdalur.

*Remarks*: The genus *Aesculus* comprises about 20 species of deciduous trees and shrubs native to temperate regions of the Northern Hemisphere, with seven to ten species native to North America and 13–15 species native in Eurasia. The fossil leaflets from Iceland are more similar to modern North American species than to those from Europe and Asia. The latter differ from the fossil by their leaf shapes (commonly obovate with a long and narrow attenuate apex) and generally distinct brochidodromous venation. Leaflets of *Aesculus* from the late Cainozoic of Europe have been compared to the modern *A. hippocastaneum* L. (Mädler 1939; Shwareva 1983; Straus 1992). Other specimens from the Neogene of Europe similar to those from Iceland have been compared to the modern North American species *A. pavia* L. and *A. flava* Ait. (*A. velitzelosii* Knobloch, Knobloch 1998). Leaflets from the Paleocene of North America (*A. hickeyi* Manchester, Manchester 2001) differ from

the Icelandic leaflets by their more widely spaced and more curved secondary veins. Schloemer-Jäger (1958) described leaflets from Early Oligocene strata of Spitsbergen with long petioles preserved that are similar to the Icelandic material by their leaf margin and shape.

### Santalaceae (Visceae)

***Viscum* aff. *album*** **P**

Plate 10.29, Figs. 10–12.

Pollen, monad, shape oblate, outline convex triangular in polar view, equatorial diameter 23–26 μm under SEM, ca 30 μm under LM, tricolpate, tectate, columellate, pollen wall ca 1.2 μm thick (LM), sculpture baculate, bacula widely spaced, smooth, surface between bacula densely covered with vertical rodlets with thickened, rounded apical parts, occurring singly or in groups (SEM); small interspaces between rodlets.

*Occurrence*: 4.2–4.0 Ma sedimentary rock formation at Tjörnes (Reká).

Remarks: Pollen grains of *Viscum album* L. figured by Feuer and Kuijt (1982) resemble the Icelandic pollen by their tectum ornamentation.

### Saxifragaceae

***Saxifraga* sp.** **P**

Plate 11.14, Figs. 1–3.

Pollen, monad, shape prolate, outline lobate in polar view, elliptic in equatorial view, polar axis 16–18 μm, equatorial diameter 9–14 μm under SEM, and 18–21 μm and ca 15 μm under LM, tricolpate, colpi ca 15 μm long (SEM), 14–18 μm (LM); eutectate, columellate, pollen wall 0.7 μm thick (LM), sculpture striate, microechinate, striae parallel, 0.5–1 μm wide, 3–8 μm long, changing orientation across pollen surface (SEM).

*Occurrence*: 1.7 Ma sedimentary rock formation at Bakkabrúnir.

*Remarks*: Very similar pollen types occur in modern species of *Saxifraga* (Verbeek-Reuvers 1977).

### Scrophulariaceae

**aff. *Euphrasia* vel *Melampyrum* sp.** **M**

Plate 8.16, Fig. 1.

Leaf, sessile, lamina ovate-elliptic, >4 mm long, 4.3 mm wide, base cuneate, apex not preserved, prominent midvein, secondary veins irregularly spaced, splitting and

their branches either supplying a basal tooth or merging with other branches, margin with distinct elongate teeth in basal part of lamina, entire in apical part.

*Occurrence*: 7–6 Ma sedimentary rock formation at Brekkuá.

*Remarks*: The single leaf specimen resembles bract leaves in species of *Melampyrum* and *Euphrasia*.

**Scrophulariaceae gen. et spec. indet. (aff. *Verbascum* sp.)** **P**

Plate 11.47, Figs. 7–9.

Pollen, monad, shape spheroidal, outline lobate in polar view, circular in equatorial view, polar axis ca 21 μm, equatorial diameter ca 22 μm under SEM, ca 22 μm and 23 μm under LM, tricolporate, colpi ca 16 μm long (LM), tectate, columellate, pollen wall ca 2 μm thick, thickest in mesocolpium (LM), sculpture reticulate, muri half-spherical in cross-section, muri smooth, columellae high, aperture membrane covered with granulae (SEM).

*Occurrence*: 0.8 Ma sedimentary rock formation at Svínafell.

**Smilacaceae**

***Smilax* sp.** **M**

Plate 5.22, Figs. 1–2; 6.42, Figs. 1–3.

2005 *Smilax* sp. – Denk et al.: p. 404, figs. 175–181.

Fragments of two 3–5-veined acute leaf apices with distinct reticulate venation forming irregular narrow meshes, and a rounded base with five basal veins arising from the petiole with steep reticulate higher-order veins between them. None has yielded cuticle structures.

*Occurrence*: 12–10 Ma sedimentary rock formations at Surtarbrandsgil (12 Ma) and Tröllatunga (10 Ma).

*Remarks*: Similar leaf impressions occur in the Miocene of Europe and have been assigned to *Smilax* (e.g. Velenovský 1881: pl. 2, fig. 23), although the closely related *Heterosmilax* may also produce equivalent foliage. Among living taxa, the North American temperate species *S. rotundifolia* L. is very similar to the fossils from Iceland.

**Sparganiaceae**

***Sparganium* sp.** **P**

Plate 9.19, Figs. 1–3; Plate 10.29, Figs. 1–3.

Pollen, monad, shape spheroidal, outline circular, diameter 18–26 μm under SEM, 22–33 μm under LM, ulcerate, ulcus ca 2 μm in diameter, aperture membrane finely

granulate; semitectate, columellate, pollen wall 1.5–1.7 μm thick (LM), sculpture heterobrochate reticulate; muri microechinate, 0.5–1 μm in diameter (SEM).

*Occurrence*: 5.5–3.8 Ma sedimentary rock formations at Selárgil (5.5 Ma) and Tjörnes (Reká, Skeifá; 4.2–3.8 Ma).

*Remarks*: Modern pollen of *Sparganium* has been described and figured by Punt (1975).

**Tiliaceae subfam. Tilioideae**

***Tilia selardalense* Grímsson, Denk and Símonarson** **M**

Plate 4.18, Figs. 5–6.

1946 *Vitis olriki* Heer – Áskelsson: p. 84, fig. 4.
1978 *Vitis* sp. – Akhmetiev et al.: pl. 1, figs. 1, 5.
2007a *Tilia selardalense* Grímsson, Denk and Símonarson – Grímsson et al.: p. 203, pl. 14–15.
2007b *Tilia selardalense* Grímsson, Denk and Símonarson – Grímsson et al.: fig. 6.

Leaves petiolate; petiole 1.9 to >4.1 cm long, lamina simple or slightly trilobed, 7.5–17.0 cm long, 5.0–13.0 cm wide, length to width ratio 1.2–1.5, wide ovate to suborbiculate, apex of lobes acuminate to acute, base cordate, deeply cordate to nearly auriculate, commonly asymmetrical, margin serrate, apical side of tooth short, sigmoid, basal side long and sigmoid, tooth apex narrowly pointed, generally curved, teeth compound, of two sizes, primary and secondary teeth similar in shape, the latter much smaller, secondary veins serving primary teeth, abmedial branches or tertiary veins serving secondary teeth, sinuses between teeth narrow to wide angular, primary venation actinodromous (palmate), 5(–7) veins diverging radially from a single point, central vein thickest, stout, usually oblique to petiole; uppermost lateral primary veins arising at angles of 31–42° from central primary vein, second pair of lateral primary veins arising at 75–96° from central primary vein, third pair at angles of 121–140°, lowest pair at angles of 165–170°; lateral primaries with up to eight conspicuous, dense subparallel abmedial branches, originating from lateral primary veins at angles of 35–70°, secondary venation craspedodromous, in some cases semicraspedodromous, secondaries regularly and densely spaced, gently curved, typically branching near the margin, up to 8 pairs of secondary veins diverging from the midvein, subopposite to alternate, arising mostly at narrow angles, 30–50°; tertiary veins percurrent, simple or forked, commonly convex to slightly sinuous, approximately 3–6 tertiary veins per 1 cm of primary or secondary vein, originating at right to acute angles from exmedial and admedial side of secondary veins, quaternary veins relatively thin, orthogonal, fifth order veins forming small areoles, areoles well-developed, generally with common orientation, mostly quadrangular, no veinlets visible; light areas in axils of primary veins and between primary and secondary veins probably indicating the position of pocket domatia.

*Occurrence*: 15 Ma sedimentary rock formation at Selárdalur.

*Remarks*: *Tilia* includes around 25 modern species with a northern hemispheric distribution. The earliest fossils that can be assigned to *Tilia* are bracts from the Eocene of North America (Manchester 1999). From there the genus may have spread via the North Atlantic to Eurasia. According to Mai (1995) the genus occurs in Europe since the Oligocene. Leaf records from the European, East Asian, and North American Miocene are rare (cf. Chaney and Axelrod 1959) or confined to the bracts of fruits (e.g., Shwareva 1983; Knobloch and Kvaček 1996). The fossils described here are comparable to several extant Eurasian and North American species. *Tilia mandshurica* Rupr. and Maxim. from the Far East resembles the fossil species in the often trilobed leaves and deeply cordate base among other characters. The prominent hair tufts (pocket domatia) in the axils of primary and secondary veins, and the lobes in some of the fossil leaves are common, for instance, in the modern species *T. platyphyllos* Scop. Leaves from the Early Oligocene to Miocene of western North America assigned to *T. aspera* (Newberry) La Motte (La Motte 1936; Meyer and Manchester 1997) have a similar high number of abmedial branches of the lateral primary veins and sometimes trilobed leaves, but differ from the Icelandic forms by their smaller number of primary veins, and the wider teeth. Kvaček and Walther (2004) reported large leaves of *T. gigantea* Ettingshausen from the Early Oligocene of Bohemia. These are similar to the Icelandic leaves except that the abmedial pectinal veins are much more curved in *T. selardalense*. *Tilia saportae* Knobloch from the Pliocene of Central Europe (Knobloch 1998) has similar leaves to the Icelandic forms, but they are generally more elliptic with a less strongly cordate base.

### *Tilia* sp. P

Plate 4.18, Figs. 1–4; Plate 6.43, Figs. 1–3.

Pollen, monad, shape oblate, outline in polar view subcircular to ovoid, equatorial diameter 28–39 × 28–44 μm under SEM, 29–46 × 30–55 μm under LM, brevicolporate, colpi 6.5–8.2 μm long (SEM), semitectate, columellate, pollen wall 1.5–2 μm thick (LM), sculpture microreticulate to perforate, colpus membrane granulate (SEM).

*Occurrence*: 15–10 Ma sedimentary rock formations at Botn (15 Ma) and Tröllatunga (10 Ma).

*Remarks*: This pollen type may comprise more than a single natural species.

## Trochodendraceae

### *Tetracentron atlanticum* Grímsson, Denk and Zetter M, P

Plate 4.20, Figs. 1–3; Plate 5.23, Figs. 1–12; Plate 7.21, Figs. 1–6; Plate 8.11, Figs. 13–15; Plate 8.16, Figs. 2–3; Plate 9.19, Figs. 4–6, Plate 10.29, Figs. 4–6.

2008 *Tetracentron atlanticum* Grímsson, Denk and Zetter – Grímsson et al.: p. 3, fig. 2, B, E, fig. 3, A, F, J, O, P, fig. 4, fig. 5, A–C.
2008a *Tetracentron atlanticum* Grímsson, Denk and Zetter – Grímsson and Símonarson: fig. 5.

Leaves petiolate; petiole up to 4.5 cm long, stout; lamina up to 12.4 cm long and 9.5 cm wide, asymmetrical or symmetrical, wide ovate to wide elliptic, length to width ratio ca 1.2/1, length of petiole to length of lamina ca 0.27/1 (measured in a single specimen); apex acute to acuminate, base cordate to lobate; extreme base entire-margined, margin serrate, evenly toothed, apical side of tooth concave to acuminate, basal side convex to acuminate, tooth with elongate apex, curving upwards, tooth acumen glandular, teeth relatively large, 4–8 teeth per 2 cm margin, sinuses usually angular, rarely rounded, principal veins entering teeth medially, two distinct veins connecting glandular region of tooth to adjacent sinuses; primary venation actinodromous, 5–7 veins, central primary vein straight in proximal part, two or three pairs of lateral primary veins, innermost primary veins forming angles of 22–27° with central vein, second pair of primary veins forming angles of 45–65° with central vein, outermost primary veins forming angles of 85–95° with central vein, lateral primary veins running in strongly developed recurved arches, converging with other veins towards leaf apex; secondary veins brochidodromous and connecting to superadjacent secondary veins, secondary veins diverging from midvein at 30–40°, branches of secondary or higher order loops running into sinuses of teeth and tooth apex; tertiary veins originating at right to acute angles from primary or secondary veins and their branches, tertiary veins thin but distinct, irregularly percurrent, simple or forked; quaternary veins orthogonal, arising at right angles, marginal ultimate venation looped, areoles well developed, moderate to large, 0.76–1.52 mm across, irregular in size and shape, veinlets slender, branched two to three times.

Fruits detached capsules, eroded, compressed, two of four carpels visible, up to 3.9 mm long and 3 mm wide, length to width ratio approximately 1.28; apex emarginate, fruit with a median axial lineation; styles persistent, originating in lower third part of fruit, one style per carpel, styles broken in all specimens, style parts >0.7 mm long, recurved; sepals preserved as imprint just below styles, alternating with styles, four sepals originally covering lowest part of fruit.

Pollen, monad, in groups of 2–14, shape subprolate, outline elliptic in equatorial view, trilobate outline in polar view, polar axis 11–17 μm, equatorial diameter 8–17 μm under SEM, 14–20 μm and 10–18 μm under LM, tricolpate, colpi 8–13 μm long (SEM), 8–13 μm (LM), aperture membrane beset with globular elements; pollen tectate to semitectate, columellate, pollen wall 0.7–0.8 μm thick (LM), sculpture striate to striatoreticulate (SEM).

*Occurrence*: 15–4.0 Ma sedimentary rock formations at Botn (15 Ma), Surtarbrandsgil (12 Ma), Húsavíkurkleif (10 Ma), Hrútagil, Torffell (9–8 Ma), Brekkuá, Hestabrekkur (7–6 Ma), Selárgil (5.5 Ma) and Tjörnes (Egilsgjóta, Reká; 4.3–4.0 Ma).

## Ulmaceae

### *Ulmus* sp. MT 1 M

Plate 4.19, Figs. 7–9.

2007a *Ulmus* sp. – Grímsson et al.: p. 205, pl. 16.
2007b *Ulmus* sp. – Grímsson et al.: fig. 4, a–f.

Lamina 5.0–6.6 cm long, 2.6–3.6 cm wide, length to width ratio 1.5–2.2, widest in middle part, ovate to narrow ovate, symmetrical; base slightly cordate, margin serrate, teeth compound, primary teeth large, served by secondary veins, with acute apex, long apical and basal sides, basal side slightly longer, apical side straight to acuminate, basal side acuminate; secondary teeth basal to primary teeth, smaller, served by external veins, basal side longer than apical side, sinuses between primary and secondary teeth deeply acute, primary venation pinnate, midvein moderate, straight, secondary venation craspedodromous, >12 pairs diverging from midvein at angles of 57–30°, straight or curved upwards, a few secondary veins forked, around 10–12 secondary veins per 5 cm of midvein, tertiary veins percurrent, forming ± right angles with secondary veins, mostly forked, some simple, oblique to midvein, becoming perpendicular in distal parts of lamina, ca 10 tertiary veins along 1 cm secondary vein, prominent tertiary veins near margin ending in sinus between two teeth.

*Occurrence*: 15 Ma sedimentary rock formation at Selárdalur.

*Remarks*: *Ulmus* incorporates around 25 species in the Northern Hemisphere (Grudzinskaya 1979; Wiegrefe et al. 1994). The genus has a fossil record dating back to the Late Cretaceous (Chmura 1973; pollen) and Paleocene/Eocene (Manchester 1989; Feng et al. 2003; fruits and leaves). The Icelandic leaves do not allow any closer comparison to a particular modern section within *Ulmus* but clearly differ from the sections *Blepharocarpus* Dumort. (highly compound teeth) and *Lanceifolia* (C. Schneider) Grudzinskaya (evergreen leaves with brochidodromous–semicraspedodromous venation).

These elm leaves differ from leaves of *Ulmus* sp. cf. *U. pyramidalis* Goepp. with simple coarsely dentate margins from Surtarbrandsgil (12 Ma; Denk et al. 2005). Because modern species of *Ulmus* have extremely variable leaves depending on their position on the tree (sun exposed versus shadow, short vs. long shoots, vegetative vs. fertile shoots) a lot more material would be needed to clarify the status of these remains.

### *Ulmus* sp. MT 2 M

Plate 7.22, Figs. 1–2.

Leaf, petiole not preserved, lamina elliptic, 3.8 cm long and 2.2 cm wide, length to width ratio 1.73, base slightly asymmetrical, obtuse, apex acute, margin serrate, teeth compound, basal and apical sides convex to acuminate, primary teeth of the

same size, often with minute subsidiary teeth on basal side, secondary venation craspedodromous, 9–10 pairs of secondary veins that are forked in lower and middle part of lamina, secondary veins diverging from midvein at angles of 60–40°, tertiary veins percurrent, simple or forked, 7 per 1 cm of secondary vein, trichome bases equally distributed on coastal area appearing as small protrusions.

*Occurrence*: 9–8 Ma sedimentary rock formation at Hrútagil.

*Remarks*: The typical trichome bases seen in the fossil are also present on the adaxial leaf surface of the modern species *Ulmus glabra*.

### *Ulmus* section *Ulmus* sp. M

Plate 7.22, Figs. 3–4.

2005 *Ulmus* sp. – Grímsson et al.: p.18, fig. 2, b.

Samara, endocarp with wing 3.6 cm long and 2.3 cm wide, pedicel and basal part of calyx 3 mm long, calyx 4.4 mm long and 3.3 mm wide, calyx funnel-shaped, free lobes of calyx comprising ca half of calyx, endocarp close to the centre of samara, 7.5–9 mm long and 6.5–7 mm wide, apical notch of wing ca 6 mm deep, samara venation radiating.

*Occurrence*: 9–8 Ma sedimentary rock formation at Hrútagil.

*Remarks*: The samaras clearly belong to section *Ulmus* sensu Wiegrefe et al. (1994).

### *Ulmus* sp. cf. *U. pyramidalis* Goepp. M

Plate 5.22, Figs. 3–7.

1954 *Zelkova* cf. *ungeri* Kovats – Áskelsson: p. 95, fig. 8.
2005 *Ulmus* cf. *pyramidalis* Goepp. – Denk et al.: p. 404, figs. 182–188.

Lamina 3.5–7 cm long, 1.6–2.6 cm wide, base asymmetric, petiole 6–8 mm long, with simple coarsely dentate margin and partly forked secondaries.

*Occurrence*: 12 Ma sedimentary rock formation at Surtarbrandsgil.

*Remarks*: These leaves belong undoubtedly to the Ulmaceae. We compare them to a common Miocene elm of Europe, *U. pyramidalis* Goepp., from which they differ in having slightly more widely spaced secondaries and a longer petiole.

### *Ulmus* sp. P

Plate 4.19, Figs. 1–6; Plate 6.43, Figs. 4–6; Plate 7.21, Figs. 7–12.

Pollen, monad, shape oblate, outline polygonal in polar view, equatorial diameter 24–36 μm under SEM, 27–42 μm under LM, pollen stephanoporate (5–6), porus 1.3–3.8 μm in diameter (SEM, LM), eutectate, columellate, pollen wall 0.6–1.3 μm thick (LM), sculpture rugulate, rugulae covered with microechinae (SEM).

*Occurrence*: 15–8 Ma sedimentary rock formations at Botn (15 Ma), Tröllatunga, Húsavíkurkleif (10 Ma) and Hrútagil (9–8 Ma).

*Remarks*: This taxon most likely comprises more than a single natural species. Pollen in modern *Ulmus* may be markedly similar among different species (see, for example, Stafford 1995).

**aff. *Cedrelospermum* sp.** **P**

Plate 5.22, Figs. 8–10.

Pollen, monad, shape oblate, outline quadrangular in polar view, equatorial diameter 18–19 μm under SEM, 19–20 μm under LM, tetraporate, tectate, columellate, sculpture verrucate (LM, SEM), verrucae with microechinate suprasculpture (SEM).

*Occurrence*: 12 Ma sedimentary rock formation at Surtarbrandsgil.

**Valerianaceae**

***Valeriana* sp.** **M**

Plate 11.26, Fig. 6.

1978 *Phyllites* cf. *Valeriana officinalis* L. foss. – Akhmetiev et al.: pl. 16, figs. 7, 8.

Leaflet, lamina ca 2.4 cm long, 7 mm wide, length to width ratio 3.5, lamina slightly asymmetrical, base asymmetrical, narrow elliptic, margin entire but possibly irregularly dentate, one tooth preserved, secondary venation irregular brochidodromous to eucamptodromous, secondary originating in regular intervals on one side of lamina, at least five veins, a single secondary vein on other side of lamina, running subparallel to primary vein towards apex, several branches of secondary vein running towards margin, tertiary veins running from primary vein to the single secondary vein, or running parallel to primary vein and connecting two adjacent secondary veins.

*Occurrence*: 1.1 Ma sedimentary rock formation at Stöð.

**aff. *Valeriana* sp.** **P**

Plate 9.19, Figs. 7–9; Plate 10.29, Figs. 7–9.

Pollen, monad, shape oblate to spheroidal, outline lobate in polar view, elliptic outline in equatorial view, polar axis 39–40 μm, equatorial diameter 23–53 μm under SEM, polar axis 28–48 μm, equatorial diameter 31–65 μm under LM, tricolpate, colpi ca 20 μm long (LM); tectate, columellate, pollen wall 1.6–2 μm thick (LM), sculpture perforate, echinate; echinae irregularly spaced, each echinus situated on a distinct hemispherical halo of 3–5 μm diameter; surface between haloes in some cases with microechinae (SEM); aperture membrane covered with granulae.

*Occurrence*: 5.5–3.8 Ma sedimentary rock formations at Selárgil (5.5 Ma) and Tjörnes (Egilsgjóta, Reká, Skeifá; 4.3–3.8 Ma).

*Remarks*: Punt et al. (2007) defined 'halo' as a "zone around a well-defined feature such as a spine or an aperture". Here, we use halo for the thickened base of the echinae in *Valeriana*. In contrast, Clarke (1978) stated that the halo is peculiar to Valerianaceae, being "a bright band round the margin of the aperture". Pollen closely resembling our specimesn is figured in Clarke and Jones (1977b).

**Valerianaceae gen. et spec. indet.** **P**

Plate 5.23, Figs. 13–15.

Pollen, monad, shape spheroidal, outline subcircular in equatorial view, polar axis ca 25 μm, equatorial diameter ca 21 μm under SEM, ca 28 μm and 24 μm under LM, tricolpate, colpi ca 17 μm long (SEM), ca 18 μm (LM), tectate, columellate, pollen wall 1.3–1.5 μm thick (LM), sculpture microechinate, perforate (SEM).

*Occurrence*: 12 Ma sedimentary rock formation at Surtarbrandsgil.

**Vitaceae**

***Parthenocissus* sp.** **P**

Plate 4.20, Figs. 4–6; Plate 6.43, Figs. 7–9.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis 29–34 μm, equatorial diameter 18–22 μm under SEM, 34–37 μm and 23–27 μm under LM, tricolporate, colpi 22–26 μm long (SEM), 29–31 μm (LM), tectate, columellate, pollen wall 1.4–2.3 μm thick (LM), thickest in polar area, sculpture microreticulate to reticulate (SEM).

*Occurrence*: 15–10 Ma sedimentary rock formations at Botn (15 Ma) and Tröllatunga (10 Ma).

Remarks: This morphotaxon may belong to two different species.

**Incertae Sedis – Magnoliophyta**

**Angiosperm fam. gen. et spec. indet. A** **M**

Plate 7.23, Figs. 1–4.
Inflorescence; catkin composed of numerous flowers, flowers sessile or shortly stalked.

*Occurrence*: 9–8 Ma sedimentary formation at Hrútagil.

**Angiosperm fam., gen. et spec. indet. B** **M**

Plate 8.16, Fig. 4.

Numerous slender axes with many lanceolate, awl-shaped leaves, axis 0.3–0.6 mm in diameter, leaves either in whorls or spirally arranged, 1–2.5 mm long.

*Occurrence*: 7–6 Ma sedimentary rock formation at Hestabrekkur and Brekkuá.

*Remarks*: The habit of this plant and its abundant and exclusive presence in certain stratigraphic units of the lacustrine sedimentary rocks suggest that it was an aquatic element.

**Angiosperm fam., gen. et spec. indet. C** **M**

Slender axes with lateral axes arranged in whorls, each lateral axis with whorls of hair-like structures.

*Occurrence*: 3.9–3.8 Ma sedimentary rock formation at Tjörnes (Skeifá).

***Dicotylophyllum* sp. A (‘*Neolitsea*’)** **M**

Plate 5.24, Fig. 4.

2005 *Dicotylophyllum* sp. 3 (‘*Neolitsea*’) – Denk et al.: p. 408, fig. 209.

A single leaf, lamina elliptic, entire, >8 cm long, 2.5 cm wide, no petiole preserved, base probably acute, apex bluntly acute, modified acrodromous, i.e. three primary veins merged along ca 1 cm from the leaf base, lateral primary veins connected with secondary veins in the upper third of the leaf and forming a brochidodromous pattern, short secondary veins originating from lateral primary veins and running to the leaf margin.

*Occurrence*: 12 Ma sedimentary rock formation at Surtarbrandsgil.

*Remarks*: Similar leaves occur in *Neolitsea* (Lauraceae). Without information about epidermal features, however, a closer comparison to modern genera is greatly hampered.

***Dicotylophyllum* sp. B** **M**

Plate 6.42, Figs. 6–7.

2005 *Dicotylophyllum* sp. 4 – Denk et al.: p. 408, figs. 210–212.

Leaf fragment, elliptic, dentate, ca 8.5 cm long, 3 cm wide, base not preserved (? acute), apex elongate acute to acuminate, secondary venation brochidodromous, primary loops followed by a series of higher-order loops, teeth spinose with glandular tip, basal side convex, much longer than apical side.

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

*Remarks*: A distinct leaf type, which we are not able to assign to any living family.

***Dicotylophyllum* sp. C** **M**

Plate 6.42, Figs. 4–5.

2005 *Dicotylophyllum* sp. 5 – Denk et al.: p. 410, figs. 213, 214.

Leaves, 5.5–6 cm long, 2.5 cm wide, ovate-elliptic, dentate, secondary venation brochidodromous, primary loops followed by secondary loops from which small veinlets supply the spinose teeth.

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

*Remarks*: A distinct leaf type, which we are not able to assign to any living family. Dentition resembles some species of *Pyrus* L. within the Rosaceae.

***Dicotylophyllum* sp. D** **M**

Plate 7.23, Fig. 5.

Seedling with two or three leaves; twiglets decussate, leaves on apical parts of lateral and main branches, lamina 1.6–1.7 cm long and 7–15 mm wide, elliptic, secondary veins irregularly spaced, venation semicraspedodromous to craspedodromous, margin entire to dentate, teeth irregularly spaced.

*Occurrence*: 9–8 Ma sedimentary formation at Hrútagil.

***Dicotylophyllum* sp. E** **M**

Plate 7.23, Fig. 6.

Leaf or leaflet, no petiole preserved, lamina ca 7.5 cm long, 2.3 cm wide, narrow elliptic, base cordate, margin entire, secondary venation camptodromous to brochidodromous, secondary veins irregularly spaced, 0–2 intersecondary veins present, 13 pairs of secondary veins.

*Occurrence*: 9–8 Ma sedimentary formation at Hrútagil.

**Monocotyledonae fam. et. gen. indet. sp. 1** **P**

Plate 10.30, Figs. 1–3.

Pollen, monad, shape oblate, outline elliptic (boat shaped) in polar view, polar axis ca 18 μm, equatorial diameter ca 30 μm under SEM, ca 23 μm and 35 μm under LM, sulcate, semitectate, sculpture rugulate-perforate (SEM).

*Occurrence*: 3.9–3.8 Ma sedimentary rock formation at Tjörnes (Skeifá).

**Monocotyledonae fam. et. gen. indet. sp. 2** **P**

Pollen, monad, shape oblate, outline elliptic in equatorial view, polar axis ca 19 μm, equatorial diameter, ca 32 μm under SEM, ca 22 μm and ca 40 μm under LM, sulcate, semitectate, sculpture psilate-perforate (SEM).

*Occurrence*: 1.1 Ma sedimentary rock formation at Stöð.

**Pollen type 1 (?Euphorbiaceae)** **P**

Plate 4.20, Figs. 7–12; Plate 5.25, Figs. 1–6.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis 23–30 µm, equatorial diameter 18–23 µm under SEM, 27–35 µm and 23–25 µm under LM, tricolporate, colpi 15–23 µm long (SEM), eutectate, columellate, pollen wall 1.3–1.7 µm thick (LM), sculpture rugulate perforate, fusing at colpus area and forming a smooth rim (margo) with perforations and fossulae (SEM).

*Occurrence*: 15–12 Ma sedimentary rock formations at Botn (15 Ma) and Surtarbrandsgil (12 Ma).

**Pollen type 2 (?Cupressaceae)** **P**

Plate 5.25, Figs. 7–12.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis 32–36 µm, equatorial diameter 19–25 µm under SEM, 42– 45 µm and 27–32 µm under LM, possibly tricolpate, colpi ca 31 µm (SEM), tectate, columellate, pollen wall ca 1.3 µm thick (LM), sculpture microverrucate.

*Occurrence*: 12 Ma sedimentary rock formation at Surtarbrandsgil.

**Pollen type 3** **P**

Plate 5.26, Figs. 1–3.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis ca 21 µm, equatorial diameter ca 15 µm under SEM, ca 27 µm and 19 µm under LM, tricolpate, colpi ca 17 µm long (SEM), tectate, columellate, pollen wall 1–1.2 µm thick (LM), sculpture microrugulate-perforate (SEM).

*Occurrence*: 12 Ma sedimentary rock formation at Surtarbrandsgil.

**Pollen type 4** **P**

Plate 5.26, Figs. 4–6.

Pollen, monad, shape spheroidal, outline subcircular in polar view, polar axis ca 18 µm, equatorial diameter ca 19 µm under SEM, ca 21 µm and 23 µm under LM, (?) tricolpate, tectate, columellate, pollen wall 1.3–1.5 µm thick (LM), sculpture irregularly verrucate; verrucae of variable size, smaller in mesocolpium (SEM).

*Occurrence*: 12 Ma sedimentary rock formation at Surtarbrandsgil.

**Pollen type 5** **P**

Plate 5.26, Figs. 7–9.

Pollen, monad, shape subprolate, outline elliptic in equatorial view, polar axis ca 28 μm, equatorial diameter ca 22 μm under SEM, ca 34 μm and 28 μm under LM, aperture type?, tectate, columellate, pollen wall ca 0.9 μm thick (LM), sculpture microverrucate, microechinate (SEM).

*Occurrence*: 12 Ma sedimentary rock formation at Surtarbrandsgil.

**Pollen type 6** **P**

Plate 5.26, Figs. 10–12.

Pollen, monad, shape subspheroidal, outline subcircular in equatorial view, polar axis ca 25 μm, equatorial diameter ca 19 μm under SEM, ca 30 μm and ca 25 μm under LM, type of aperture?, tectate, columellate, sculpture microverrucate, microechinate (SEM).

*Occurrence*: 12 Ma sedimentary rock formation at Surtarbrandsgil.

**Pollen type 7 (?*Lemna* sp.)** **P**

Plate 5.27, Figs. 1–3.

Pollen, monad, shape spheroidal, outline circular, diameter 25–30 μm under SEM, 28–33 μm under LM, (?) ulcerate, tectate, columellate, sculpture echinate (SEM).

*Occurrence*: 12 Ma sedimentary rock formation at Surtarbrandsgil.

**Pollen type 8** **P**

Plate 6.44, Figs. 1–3.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis ca 14.5 μm, equatorial diameter ca 11 μm under SEM, ca 18 and ca 14 μm under LM, tricolporate, colpi 11–12 μm long (SEM), tectate, columellate, sculpture microverrucate, tectum arching over porus (SEM).

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

**Pollen type 9 (*Gentiana, Aesculus*)**

Plate 6.44, Figs. 4–6.

Pollen, monad, shape spheroidal, polar axis ca 23 μm, equatorial diameter ca 22 μm under SEM, ca 35 μm and ca 31 μm under LM, tricolporate, colpi 26–27 μm

(LM), 20–21 μm (SEM) long, eutectate, columellate, pollen wall 1.6–2 μm thick (LM), sculpture striate, striae layered and appearing interwoven (SEM).

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

*Remarks*: Tricolporate pollen grains with similar striate sculpturing are found in Gentianaceae (Punt and Nienhuis 1976; Buchner and Weber 2000) and *Aesculus* (Heath 1984; Pozhidaev 1995).

**Pollen type 10** **P**

Plate 6.44, Figs. 7–9.

Pollen, monad, shape prolate, polar axis ca 26 μm, equatorial diameter ca 16 μm under SEM, ca 28 μm and ca 19 μm under LM, tricolpate, colpi ca 24 μm (SEM), ca 22 (LM), eutectate, columellate, pollen wall ca 1.4 μm thick (LM), sculpture striato-reticulate, striae forming a network, lumina trigonal to pentagonal.

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

**Pollen type 11** **P**

Plate 6.44, Figs. 10–13.

Pollen, monad, shape suboblate, outline elliptic in equatorial view, subcircular in polar view, polar axis ca 23 μm, equatorial diameter ca 21 μm under SEM, ca 25 μm and 28 μm under LM, tricolporate, colpi ca 19 μm (SEM), ca 20 μm (LM), eutectate, columellate, pollen wall 1.7–2.1 μm thick (LM), sculpture rugulate-perforate; rugulae longer in mesocolpium and shorter close to apertures, aperture membrane granulate.

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

**Pollen type 12** **P**

Plate 6.45, Figs. 1–3.

Pollen, monad, shape subprolate, outline elliptic in equatorial view, polar axis ca 25 μm, equatorial diameter ca 21 μm (SEM), ca 28 μm and 23 μm under LM, tricolpate, colpi ca 15 μm (SEM), ca 16 μm (LM), eutectate, columellate, pollen wall ca 2.9 μm thick (LM), sculpture reticulate, columellae conspicuously high, lumina smallest adjacent to colpi, largest near poles.

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

**Pollen type 13** **P**

Plate 6.45, Figs. 4–9.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis 13–17 μm, equatorial diameter 7–10 μm under SEM, 15–18 μm and 8–12 μm under LM, tricolporate, colpi 11–15 μm long (SEM), 15 μm (LM), eutectate, columellate, pollen wall 0.9–1 μm thick (LM), sculpture psilate, perforate to microreticulate.

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

**Pollen type 14** **P**

Plate 6.45, Figs. 10–12.

Pollen, monad, shape subprolate, outline elliptic in equatorial view, polar axis ca 26 μm, equatorial diameter ca 21 μm (SEM), ca 29 μm and 25 μm under LM, tricolporate, colpi 19–20 μm long (SEM), eutectate, columellate, pollen wall ca 2.5 μm thick (LM), sculpture incomplete reticulate in mesocolpium, reticulate near poles, lumina smaller towards poles, columellae conspicuously high.

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

*Remarks*: This pollen type could be an aberrant form of Pollen type 13.

**Pollen type 15 [aff. *Aesculus* ?]** **P**

Plate 6.46, Figs. 1–3.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis ca 27 μm, equatorial diameter ca 13 μm (SEM), ca 30 μm and ca 17 μm under LM, tricolpate, colpi ca 24 μm long (SEM), 25–26 μm (LM), eutectate, columellate, pollen wall 1–1.2 μm thick (LM), sculpture striate, striae radiating from colpi, striae 0.1–0.3 μm wide, divided by narrow grooves, striae interconnected by lateral bridges.

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

**Pollen type 16** **P**

Plate 6.46, Figs. 4–6.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis ca 27 μm, equatorial diameter ca 13 μm (SEM), ca 30 μm and 16 μm under LM, tricolpate, colpi ca 23 μm long (SEM), ca 23 μm (LM), eutectate, columellate, pollen

wall ca 1.1 μm thick (LM), sculpture microreticulate, muri 0.5–0.8 μm wide, smooth, lumina small.

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

**Pollen type 17 (?Cupressaceae)** **P**

Plate 6.46, Figs. 7–9.

Pollen, monad, outline elliptic, dimensions ca 15 × 12 μm under SEM, ca 17 × 15 μm under LM, sculpture microverrucate, granulate.

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

*Remarks*: This pollen type resembles pollen of Taxodiaceae.

**Pollen type 18** **P**

Plate 6.46, Figs. 10–12.

Pollen, monad, shape spheroidal, outline subcircular in equatorial view, equatorial diameter 23–24 μm (SEM), polar axis ca 23 μm, equatorial diameter ca 245 μm under LM, tricolpate, eutectate, columellate, sculpture microverrucate, perforate, verrucae with granula.

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

**Pollen type 19** **P**

Plate 6.47, Figs. 1–3.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis ca 34 μm, equatorial diameter ca 21 μm (SEM), ca 35 μm and 23 μm under LM, tricolpate, colpi ca 30 μm long (SEM), eutectate, columellate, pollen wall 1.2–1.5 μm thick (LM), sculpture microreticulate, lumina roundish.

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

**Pollen type 20** **P**

Plate 6.47, Figs. 4–6.

Pollen, monad, shape prolate, outline elliptic in equatorial view, polar axis ca 18 μm, equatorial diameter ca 12 μm (SEM), ca 19 μm and 12 μm under LM, tricolporate, colpi ca 15 μm long (SEM), eutectate, columellate, pollen wall ca 0.6–0.7 μm thick (LM), sculpture microechinate, perforate.

*Occurrence*: 10 Ma sedimentary rock formation at Tröllatunga.

**Pollen type 21** **P**

Plate 9.20, Figs. 1–3.

Pollen, monad, shape suboblate, outline lobate in polar view, elliptic in equatorial view; equatorial diameter ca 21 μm (SEM), ca 23 μm and 27 μm under LM, tricolporate, colpi ca 19 μm long (LM), eutectate, columellate, pollen wall 1.2–1.5 μm thick (LM), sculpture rugulate, fossulate.

*Occurrence*: 5.5 Ma sedimentary rock formation at Selárgil.

**Pollen type 22** **P**

Plate 9.20, Figs. 4–6.

Pollen, monad, shape prolate, outline lobate in polar view, elliptic in equatorial view; polar axis ca 20 μm, equatorial diameter ca 16 μm (SEM), ca 24 μm and 21 μm under LM, tricolporate, colpi ca 14 μm long (SEM), ca 19 μm (LM), eutectate, columellate, pollen wall 1.3 μm thick (LM), sculpture rugulate/microrugulate-perforate, smooth along colpi.

*Occurrence*: 5.5 Ma sedimentary rock formation at Selárgil.

**Pollen type 23** **P**

Plate 9.20, Figs. 7–9.

Pollen, monad, shape prolate, outline elliptic in equatorial view; polar axis ca 27 μm, equatorial diameter ca 20 μm (SEM), ca 31 μm and 24 μm under LM, tricolporate, colpi 22–23 μm long (SEM), eutectate, columellate, pollen wall 1.2–1.5 μm thick (LM), sculpture perforate and segmented (SEM).

*Occurrence*: 5.5 Ma sedimentary rock formation at Selárgil.

**Pollen type 24 (?*Filipendula*)** **P**

Plate 10.30, Figs. 4–9.

Pollen, monad, shape prolate, outline lobate in polar view, elliptic in equatorial view; polar axis 18–22 μm, equatorial diameter 12–16 μm (SEM), 23–25 μm and 17–22 μm under LM, tetracolporate, colpi 10–12 μm long (SEM), 13–17 μm (LM), eutectate, columellate, pollen wall 1.3–1.7 μm thick (LM), sculpture microechinate (SEM).

*Occurrence*: 4.3–4.2 Ma sedimentary rock formation at Tjörnes (Egilsgjóta).

**Pollen type 25 (?Rosaceae)** **P**

Plate 10.30, Figs. 10–12.

Pollen, monad, shape subprolate, outline rhombic in equatorial view; polar axis ca 11 μm, equatorial diameter ca 11 μm (SEM), ca 14 μm and 15 μm under LM, tricolporate, colpi ca 9 μm long (SEM), 10–11 μm (LM), eutectate, columellate, pollen wall ca 0.7 μm thick (LM), sculpture striate, sexine arching over porus from both sides(bridge).

*Occurrence*: 4.3–4.2 Ma sedimentary rock formation at Tjörnes (Egilsgjóta).

**Pollen type 26** **P**

Plate 10.30, Figs. 13–15.

Pollen, monad, shape prolate, outline elliptic equatorial view; polar axis ca 25 μm, equatorial diameter ca 15 μm (SEM), ca 32 μm and ca 19 μm under LM, tricolporate, colpi ca 19 μm long (SEM), ca 24 μm (LM), eutectate, columellate, pollen wall 1–1.3 μm thick (LM), sculpture striate, perforate fossulate (SEM).

*Occurrence*: 4.3–4.2 Ma sedimentary rock formation at Tjörnes (Egilsgjóta).

**Pollen type 27** **P**

Plate 10.31, Figs. 1–6.

Pollen, monad, shape spheroidal, outline circular; diameter 24–29 μm (SEM), 28–30 μm under LM, pantocolporate, number of colpi observed 18–21; colpi ca 6 μm long (SEM), 10–11 μm (LM), eutectate, columellate, pollen wall 1.3–1.5 μm thick (LM), sculpture densely microverrucate, echinate, echinae composed of fused bundles.

*Occurrence*: 4.2–4.0 Ma sedimentary rock formation at Tjörnes (Reká).

**Pollen type 28** **P**

Plate 11.14, Figs. 4–12; Plate 11.29, Figs. 7–9.

Pollen, monad, shape spheroidal, outline circular; diameter 14–29 μm (SEM), 18–33 μm under LM, pantocolpate, number of colpi 15–18; colpi 2.7–3.7 μm long (SEM), 4–5 μm (LM); eutectate, columellate, pollen wall 1–1.5 μm thick (LM), sculpture densely microverrucate, echinate, 19–25 echinae per 50 $\mu m^2$, echinae long and narrow, their bases composed of fused bundles (SEM).

*Occurrence*: 1.7–1.1 Ma sedimentary rock formations at Bakkabrúnir (1.7 Ma) and Stöð (1.1 Ma).

**Pollen type 29** **P**

Plate 10.31, Figs. 7–9.

Pollen, monad, shape spheroidal, outline rounded, diameter 14–17 under SEM, and 20–22 μm under LM, ?tricolpate, eutectate, columellate, pollen wall ca 0.7 μm thick (LM), sculpture microrugulate-perforate, echinate, echinae 1–1.8 μm long, 0.4–0.5 μm wide at base, conical, smooth (SEM).

*Occurrence*: 4.3–4.0 Ma sedimentary rock formations at Tjörnes (Egilsgjóta, Reká).

**Pollen type 30** **P**

Plate 10.31, Figs. 10–12.

Pollen, monad, shape oblate, outline circular; diameter 24–29 μm (SEM), 28–33 μm under LM, stephanoporate (6) annulate, pori 0.8–1.4 μm diameter (SEM); eutectate, columellate, pollen wall 1.3–1.6 μm thick (LM), sculpture verrucate, microechinate.

*Occurrence*: 3.9–3.8 Ma sedimentary rock formation at Tjörnes (Skeifá).

**Pollen type 31 (?Ranunculaceae)** **P**

Plate 11.29, Figs. 10–12.

Pollen, monad, shape spheroidal, outline circular; diameter 25–30 μm (SEM), 31–32 μm under LM, pantocolpate, number of colpi 12–14, colpi 11–12 μm long (SEM), 11–13 μm (LM); three colpi joining, mesocolpium divided in quadrangular shields; eutectate, columellate, pollen wall ca 1.6 μm thick (LM), sculpture perforate, microechinate.

*Occurrence*: 1.1 Ma sedimentary rock formation at Stöð.

**Pollen type 32** **P**

Plate 11.47, Figs. 10–12.

Pollen, monad, shape oblate, outline lobate in polar view; diameter 13–15 μm (SEM), 12–15 μm under LM, tricolpate, eutectate, columellate, pollen wall ca 1.2 μm thick (LM), sculpture densely granulate.

*Occurrence*: 0.8 Ma sedimentary rock formation at Svínafell.

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# Chapter 4
# The Archaic Floras

**Abstract** The oldest plant fossils currently known from Iceland are ca 15 Ma, their deposition coinciding with the Mid-Miocene Climatic Optimum. At this time, forests in Iceland were dominated by mixed broadleaved deciduous and coniferous taxa with a few broadleaved evergreen genera such as *Rhododendron* and *Ilex*. Lowland forests were dominated by *Glyptostrobus*. Questions about the colonization history of Iceland or proto-Iceland are of particular interest since not much is known about the availability of effective land bridges allowing for colonization from Europe and/or North America at that time. In addition to geological data, in this chapter we use two lines of biological evidence to speculate about the early colonization of Iceland. First, we will examine the biogeographic patterns of key taxa such as *Cryptomeria, Rhododendron ponticum*-type, and *Fagus friedrichii*. Then we look at dispersal modes found in early colonizers of Iceland. Dispersal modes of at least some taxa indicate that Iceland was connected to the adjacent continents at the time of colonization. However, it cannot be determined when exactly this early colonization happened. The taxa recorded in the oldest sedimentary rocks in Iceland may have had different origins, either representing elements that were already present in the region since the Palaeogene or colonizing proto-Iceland from North America/Greenland and/or Europe later in the Neogene.

## 4.1 Introduction

The oldest plant-bearing sediments of Iceland belong to the Selárdalur-Botn Formation and are ca 15 Ma (Langhian, early Middle Miocene; Moorbath et al. 1968; Kristjánsson et al. 1975, 2003; McDougall et al. 1984; Hardarson et al. 1997). Traditionally, much less attention has been paid to these sedimentary rocks than to the younger, ca 12 Ma, Brjánslækur-Seljá Formation (Heer 1859, 1868; Mai 1995; see Chap. 5). This is probably due to the much more fragmentary preservation of macrofossils from the Selárdalur-Botn Formation and the remoteness of exposures belonging to this formation. Moreover, the macrofossil record of this formation is scanty compared to the greatly richer flora from Brjánslækur. The Icelandic geologist Jóhannes Áskelsson (1946, 1956, 1957) was the first to carry out research

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on the Selárdalur flora. He compared Icelandic macrofossils to "Miocene" plant fossils from Arctic areas published by Oswald Heer in the nineteenth century. Heer had considered Arctic floras from Greenland, Spitsbergen, and Iceland to be of Miocene age (Heer 1868–1883), but later studies showed that Cainozoic sediments from Greenland and Spitsbergen were much older (Palaeocene to Oligocene; Ravn 1922; Koch 1963; Dallmann 1999). For this reason, Áskelsson (1946) introduced species such as *Vitis olriki* Heer to the flora of Iceland. The species had earlier been described from Greenland (Heer 1868). According to Budantsev (1992), this species is of uncertain taxonomic affinity, and was a typical element of boreal temperate forests in the latest Cretaceous and early Cainozoic. In the present account, leaves from Iceland that had previously been assigned to '*Vitis*', are identified as *Tilia*, which is further supported by palynological evidence. A more comprehensive account on the early Middle Miocene floras from Iceland has been provided by Akhmetiev et al. (1978), covering both macrofossils and palynological evidence using light microscopy. More recently, Grímsson and Denk (2005) and Grímsson et al. (2007) undertook a revision of macrofossils from the ca 15 Ma plant-bearing formation. This revision resulted in the recognition of several genera that had previously been unknown from the oldest sediments, such as *Aesculus, Cercidiphyllum, Platanus*, *Sequoia*, *Tilia*, and *Ulmus*. Although the Selárdalur and Botn macrofloras represent both zonal and azonal vegetation, the number of species recovered remained noticeably low compared to the younger Brjánslækur-Seljá (12 Ma, see Chap. 5) and Gautshamar-Tröllatunga Formations (10 Ma, see Chap. 6). For the present study, the palynological content of the sediments from the Botn locality was studied using both light and scanning electron microscopy resulting in a more complete picture of the Langhian floras of Iceland.

In this chapter we use evidence from both the macro- and microfossil record to discuss various scenarios of the early migration of plants to Iceland from either North America/Greenland or Europe. Moreover the Langhian floras of Iceland are briefly compared to coeval mid and high latitude floras across the northern hemisphere.

## 4.2 Geological Setting and Taphonomy

The Selárdalur-Botn Formation (15 Ma; Hardarson et al. 1997; Kristjansson et al. 2003) is exposed at the margins of the Northwest Peninsula (Fig. 4.1a, b). In the Selárdalur valley, macrofossils are found high up on Mount Þórishlíðarfjall (Fig. 4.1c; Plate 4.1). The fossil-rich sediments are ca 20 m thick and characterized by fine- to coarse-grained tuffaceous sedimentary rocks of pyroclastic origin. Generally, basaltic tuffs are most prominent, but some units contain a conspicuously high amount of white and yellowish pumice fragments. Sandstones are present in the lower to middle parts, and conglomerates in the upper parts. The sedimentary rocks and their structure indicate accumulation at moderate to high elevation (absence of fine-grained lake and river sediments) in some kind of small basin close to an active volcano. Plant remains lie both parallel to the lamination

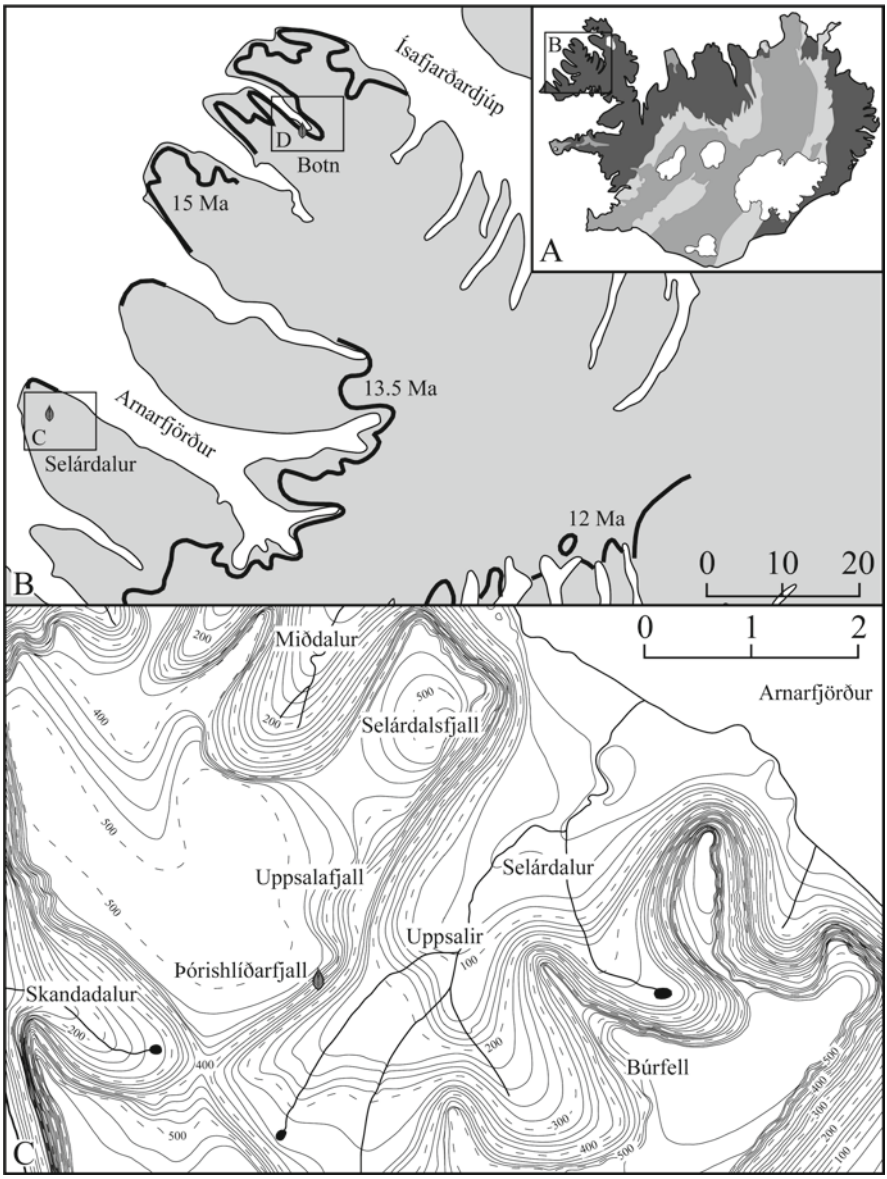



**Fig. 4.1** Map showing fossiliferous localities of the 15 Ma formation. (**a**) bedrock geology (see Fig. 1.10 for explanation), (**b**) extension of sedimentary rock formation, (**c**) Selárdalur locality, (**d**) Botn locality (Geological background modified after Jóhannesson and Sæmundsson 1989; altitudinal lines from Landmælingar Íslands 1990a, 1990b). Scale bar in kilometres

and oblique to it, and many of the fossils are folded. The orientation of the plant fossils apparently reflects transport within the sedimentary material following a pyroclastic eruption. This eruption may have swept over the trees growing in and

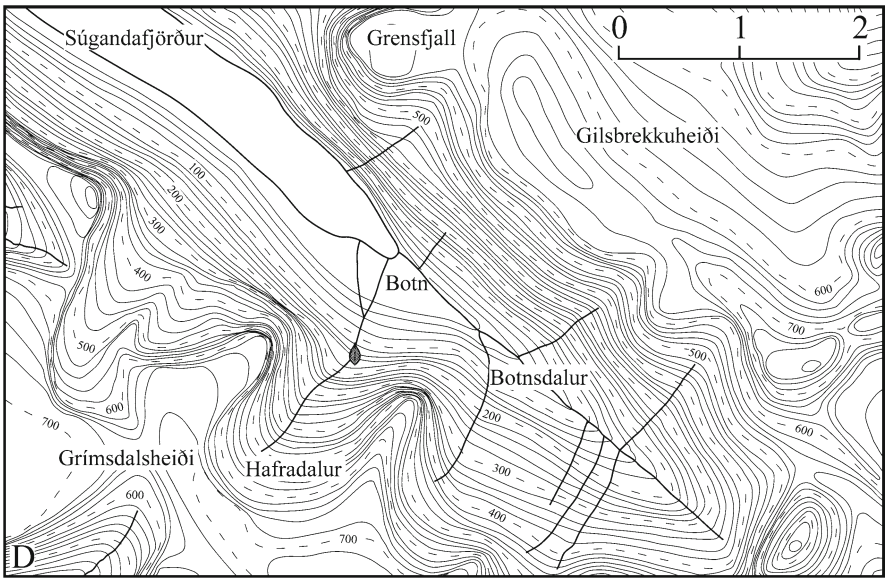



**Fig. 4.1** (continued)

around the sedimentary basin, entraining leaves in the flow. The absence of plants producing delicate leaves in the sediments and the charcoalified skeleton of the leaf venation in most leaf remains indicate that this happened under high temperature.

In the Botnsdalur valley at the base of Súgandafjörður (Fig. 4.1d; Plate 4.1), plant fossils are found close to the old lignite mine known as Botn mine or Botn locality. At the Botn locality sedimentary rocks are considerably thinner than in Selárdalur and are interpreted to reflect a lowland sedimentary environment with high groundwater level. The sediments are around 4 m thick and composed mainly of lignites with intercalated siltstones and ash layers. These sediments and their structure indicate deposition in a floodplain-dominated area with vast rivers and swamps, where organic material accumulated due to anoxic conditions. Leaves and fruits are preserved as compressions.

## 4.3 Floras, Vegetation, and Palaeoenvironments

A total of 35 taxa are recognized from the Selárdalur-Botn Formation (Table 4.1; Plates 4.2–4.20). The vast majority belong to woody angiosperms (21 taxa) and conifers (8 taxa). Lianas, herbaceous angiosperms, and ferns make up only a small fraction of the total flora (5 taxa, Fig. 4.2). In general, fewer taxa are represented by macrofossils than by pollen (11 versus 32). While pollen data give a more generalized picture of the floral content, environmental differences are

**Table 4.1** Taxa recorded for the 15 Ma floras of Iceland

| Selárdalur-Botn Formation<br>Taxa | Pollen | Leaves | RP | Cuticle | DM |
|---|---|---|---|---|---|
| Polypodiaceae | | | | | |
| *Polypodium* sp. | + | | | | 1a |
| Polypodiaceae gen. et spec. indet.1 | + | | | | 1a |
| Cupressaceae s.l. | | | | | |
| Cupressaceae gen. et spec. indet. 1 (*Cryptomeria* sp.) | + | | | | 2a |
| *Glyptostrobus europaeus* | + | **+L** | **+A** | **+** | 2a |
| Cupressaceae gen. et spec. indet. 3 (*Juniperus* sp.) | + | | | | 1b |
| *Sequoia abietina* | + | **+L** | | **+** | 2a |
| Pinaceae | | | | | |
| *Cathaya* sp. | + | | | | 2a |
| ?*Picea* sp. | | + | | | 2a |
| *Pinus* sp. 1 (Diploxylon type) | + | | | | 2a |
| *Tsuga* sp. 1 | + | | | | 2a |
| Aquifoliaceae | | | | | |
| *Ilex* sp. 1 | + | | | | 1b |
| Betulaceae | | | | | |
| *Alnus* sp. 1 | + | | | | 1a, 2a |
| *Betula* sp. 1 | + | | | | 1a |
| *Carpinus* sp. 1 | + | | | | 2a |
| Caprifoliaceae | | | | | |
| *Lonicera* sp. | | + | | | 1b |
| *Viburnum* sp. | + | | | | 1b |
| Cercidiphyllaceae | | | | | |
| *Cercidiphyllum* sp. | + | + | | | 2a |
| Ericaceae | | | | | |
| cf. *Rhododendron* sp. | | + | | | la, ?2a |
| *Rhododendron* sp. 1 | + | | | | la, ?2a |
| Fagaceae | | | | | |
| *Fagus friedrichii* | + | **+** | + D | | 2b, 3 |
| Juglandaceae | | | | | |
| *Pterocarya* sp. | + | | | | 2a |
| Liliaceae | | | | | |
| Liliaceae gen. et spec. indet. 1 | + | | | | 2a |
| Magnoliaceae | | | | | |
| cf. *Magnolia* sp. | | + | | | 1b |
| Platanaceae | | | | | |
| *Platanus leucophylla* | + | **+** | | | 2a |
| Rosaceae | | | | | |
| Rosaceae gen et. spec. indet. 1 | + | | | | 1b |
| Rosaceae gen et. spec. indet. 2 | + | | | | 1b |
| Rosaceae gen et. spec. indet. 3 | + | | | | 1b |
| *Sanguisorba* sp. | + | | | | 1b, 2a |

(continued)

**Table 4.1** (continued)

| Selárdalur-Botn Formation<br>Taxa | Pollen | Leaves | RP | Cuticle | DM |
|---|---|---|---|---|---|
| Salicaceae | | | | | |
| *Salix* sp. 1 | + | | | | 1a |
| Sapindaceae | | | | | |
| *Acer* sp. 1 | + | | | | 2a |
| *Acer* sp. 2 | + | | | | 2a |
| *Aesculus* sp. | | + | | | 2b, 3 |
| Tiliaceae | | | | | |
| *Tilia selardalense* | + | **+** | | | 1b, 2a |
| Trochodendraceae | | | | | |
| *Tetracentron atlanticum* | + | | | | 2a |
| Ulmaceae | | | | | |
| *Ulmus* sp. MT1 | + | + | | | 2a |
| Vitaceae | | | | | |
| *Parthenocissus* sp. | + | | | | 1b |
| Incertae sedis – Magnoliophyta | | | | | |
| Pollen type 1 | + | | | | ? |

*L* leafy axis, *A* fruit attached to leafy axis, *D* fruit dispersed, *RP* reproductive structure, + organ present, **+** original description of species based on this organ, *DM* Dispersal mode, *1a* wind long distance (anemochory), *1b* bird long distance (endozoochory), *2a* wind short distance (anemochory), *2b* animals short distance (exozoochory), *3* dyschory

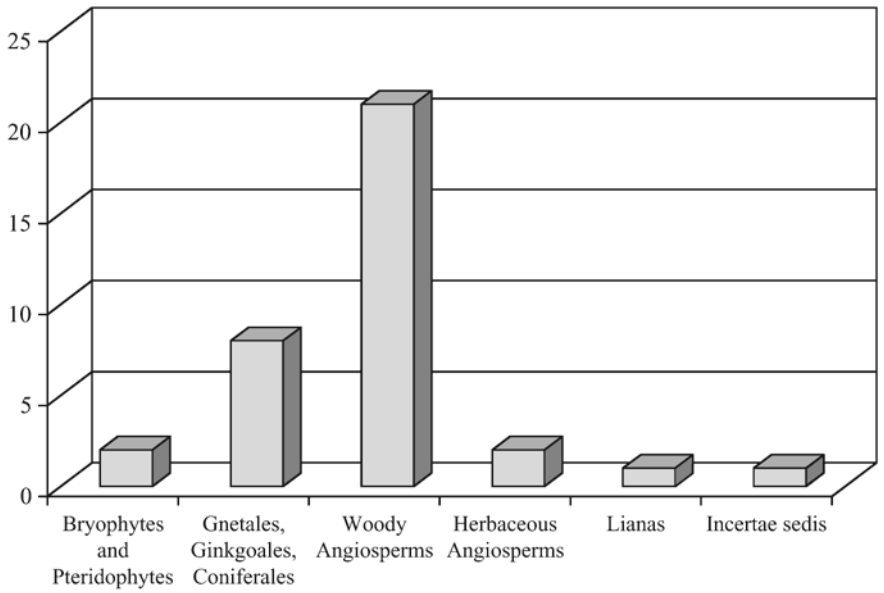



**Fig. 4.2** Distribution of life forms and higher taxa among the plants from the 15 Ma formation. Height of columns indicates number of taxa

well reflected by macrofossils from volcanic sedimentary rocks at higher elevations (Selárdalur) and from lowland alluvial plains (Botn). The former are characterized by zonal elements and dominated by *Fagus*, whereas the latter are dominated by riparian elements inhabiting swamps and hammocks (e.g. *Glyptostrobus*).

The most characteristic feature of the Selárdalur flora is the dominance of *Fagus* (>90% of the macrofossils). Other taxa include *Tilia* and *Aesculus*. The absence of azonal elements that are typically confined to lake and river environments, such as *Salix*, *Alnus*, and *Glyptostrobus* in the volcanic-pyroclastic sediments of Selárdalur points to the allochthonous or zonal character of this flora as opposed to the coeval Botn flora preserved in lignitic sediments. So far, only few macrofossil taxa have been recorded for the Botn flora. Of these, the most common ones are *Glyptostrobus* and *Sequoia*, which are represented by vegetative and fruiting twigs, whereas *Fagus* here is represented mainly by cupules and nuts, and only very few fragmentary leaves. The composition of the Botn macroflora and the sedimentary environment indicate a typical lowland flora of autochthonous origin. This lowland type of vegetation is likely to have merged into upland forests similar to the ones from Selárdalur. The combined macrofossil and palynological data allow a more differentiated reconstruction of the early Middle Miocene vegetation types and environments. Six main vegetation types can be distinguished (Table 4.2, Fig. 4.3). Azonal riparian vegetation was represented by elements from backswamp and natural levée forests. Backswamps are regularly flooded areas that are rather species poor. Typical elements of these forests were *Glyptostrobus, Pterocarya, Alnus,* and *Salix*, possibly intertwined with climbing *Parthenocissus* and forming thickets in some places (Fig. 4.4). Natural levées flanking rivers and hammocks in the floodplains are slightly more elevated areas that are only rarely exposed to inundation. Levées and hammocks were most likely inhabited by deciduous and evergreen angiosperms and lianas, such as *Acer*, *Aesculus*, *Cercidiphyllum*, *Fraxinus, Platanus*, *Ilex,* and *Parthenocissus*. Moving from the lowland riparian forests to the well-drained upland forests, the number of species increased considerably. Foothill forests may have gradually changed into montane forests (Fig. 4.5); here and there ravines with a humid micro-climate and deep soils, as well as rocky outcrops with poor soils would have occurred. Upland forests were mixed broadleaved deciduous (and evergreen) and conifer forests. In the foothills *Sequoia*, *Tsuga*, and various deciduous angiosperms (*Acer* spp., *Carpinus*) with an admixture of evergreen species (*Ilex*, possibly *Magnolia*) thrived. Higher up, montane forests were co-dominated by *Fagus, Aesculus, Tilia,* and *Ulmus* as well as conifers such as *Picea, Tsuga,* and *Cryptomeria*. *Ilex* and *Rhododendron* would have formed the understorey (Fig. 4.5). Ravine forests were probably composed of shade tolerant evergreen species (*Ilex, Rhododendron*) and rare elements such as *Cathaya*. Finally, rocky outcrop forests might have developed on poor substrates as patches within the richer upland forests but possibly also above the closed upland forests. These forests would have supplied species such as *Pinus* and the herbaceous *Sanguisorba*.

**Table 4.2** Vegetation types and their components during the mid-Miocene of Iceland. The palaeoecology of fossil species is reconstructed from their sedimentological context and ecology of modern analogues

| **Vegetation types 15 Ma** | | | |
|---|---|---|---|
| **Backswamp forests** | **Foothill forests** | **Montane forests** | **Ravine forests** |
| *Polypodium* sp. 1 | *Polypodium* sp. 1 | *Polypodium* sp. 1 | *Polypodium* sp. 1 |
| Polypodiaceae gen. et spec. indet. 1 | Polypodiaceae gen. et spec. indet. 1 | Polypodiaceae gen. et spec. indet. 1 | Polypodiaceae gen. et spec. indet. 1 |
| *Glyptostrobus europaeus* | ?*Picea* sp. | *Cryptomeria* sp. | *Cathaya* sp. |
| *Alnus* sp. 1 | *Sequoia abietina* | *Juniperus* sp. | *Aesculus* sp. |
| *Parthenocissus* sp. | *Tsuga* sp. | ?*Picea* sp. | *Ilex* sp. |
| *Pterocarya* sp. | *Aesculus* sp. | *Pinus* sp. 1 | *Acer* sp. 1 |
| *Salix* sp. 1 | *Ilex* sp. | *Tsuga* sp. | *Fagus friedrichii* |
| | *Acer* sp. 1 | *Aesculus* sp. | *Rhododendron* sp. |
| **Levée forests** | *Acer* sp. 2 | *Acer* sp. 1 | *Tilia selardalense* |
| *Polypodium* sp. 1 | *Alnus* sp. 1 | *Cercidiphyllum* sp. | *Ulmus* sp. |
| Polypodiaceae gen. et spec. indet. 1 | *Betula* sp. 1 | *Fagus friedrichii* | |
| *Aesculus* sp. | *Carpinus* sp. 1 | *Rhododendron* sp. | **Rocky outcrop forests** |
| *Ilex* sp. | *Cercidiphyllum* sp. | Rosaceae gen et. spec. indet. 1 | *Polypodium* sp. 1 |
| *Acer* sp. 2 | *Fagus friedrichii* | Rosaceae gen et. spec. indet. 2 | Polypodiaceae gen. et spec. indet. 1 |
| *Alnus* sp. 1 | *Magnolia* sp. | Rosaceae gen et. spec. indet. 3 | *Juniperus* sp. |
| *Betula* sp. 1 | *Parthenocissus* sp. | *Tetracentron atlanticum* | *Pinus* sp. 1 |
| *Carpinus* sp. 1 | *Platanus leucophylla* | *Tilia selardalense* | *Tsuga* sp. |
| *Cercidiphyllum* sp. | *Rhododendron* sp. | *Ulmus* sp. | *Cercidiphyllum* sp. |
| *Magnolia* sp. | Rosaceae gen et. spec. indet. 1 | *Viburnum* sp. | *Sanguisorba* sp. |
| *Parthenocissus* sp. | Rosaceae gen et. spec. indet. 2 | | *Tetracentron atlanticum* |
| *Platanus leucophylla* | Rosaceae gen et. spec. indet. 3 | | *Viburnum* sp. |
| *Pterocarya* sp. | *Salix* sp. 1 | | |
| *Salix* sp. 1 | *Tetracentron atlanticum* | | |
| *Ulmus* sp. | *Tilia selardalense* | | |
| | *Ulmus* sp. | | |
| | *Viburnum* sp. | | |
| **AZONAL VEGETATION** | **ZONAL VEGETATION** | | |

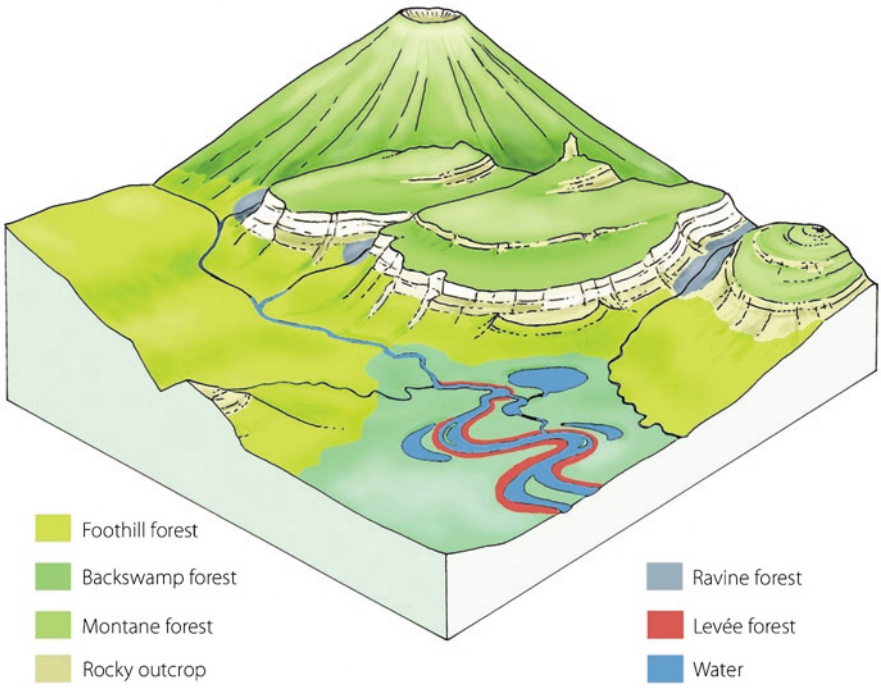



**Fig. 4.3** Schematic block diagram showing palaeo-landscape and vegetation types for the early Middle Miocene of Iceland. See Table 4.2 for species composition of vegetation types

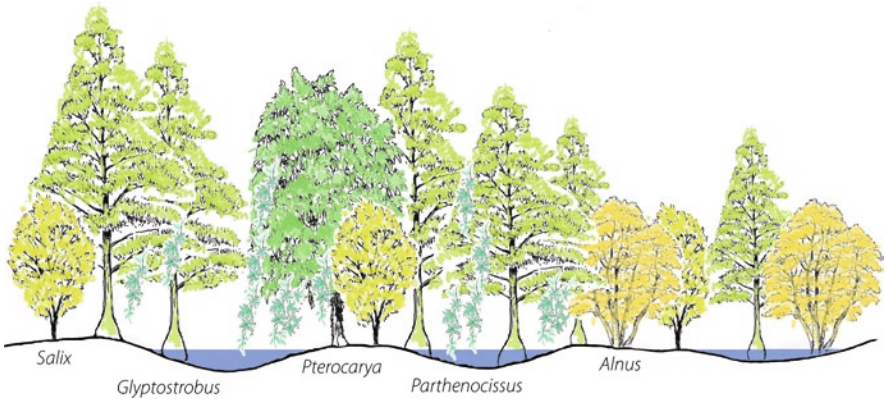



**Fig. 4.4** Schematic transect of a backswamp and levée forest

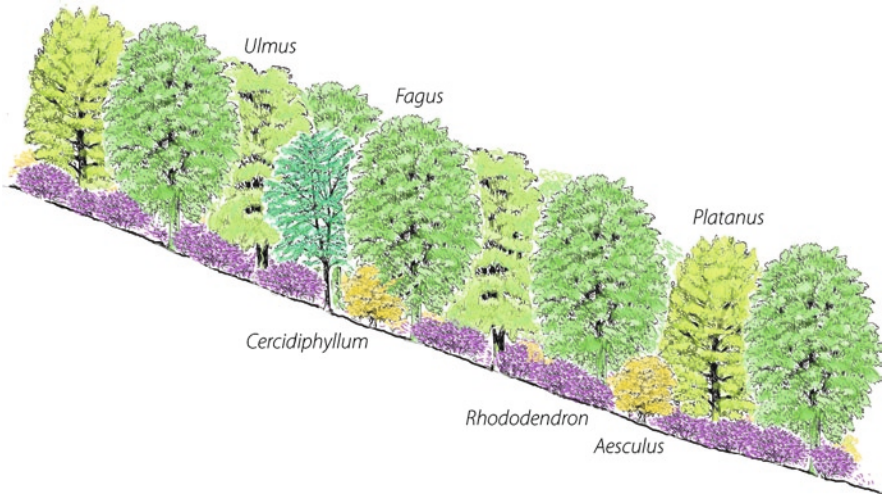



**Fig. 4.5** Schematic transect of a montane forest

## 4.4 Ecological and Climatic Requirements of Modern Analogues

Several of the taxa typical of the Selárdalur-Botn formation have modern analogues that are confined to warm, humid temperate forests of North America and Eastern Asia (see Chap. 13, Appendix 13.1) and, in some cases, have very restricted distribution ranges at present.

Some conifer species of the Selárdalur-Botn Formation belong to genera that are at present monotypic. *Cathaya* (Pinaceae) has a narrow distribution range in south Central China (Flora of China Editorial Committee 1999). The only living species, *Cathaya argyrophylla* Chun & Kuang grows in humid mountain areas on open slopes and ridges, at altitudes from 900 to 1,900 m a. s. l. It is part of evergreen broadleaved or mixed evergreen and deciduous broadleaved forests (Ying et al. 1983) thriving in a humid warm temperate climate (Cfa climate; Köppen and Geiger 1928; Köppen 1936; Kottek et al. 2006) with mean annual temperatures (MAT) of 9.3–18.6°C.

The monotypic *Glyptostrobus* is an element of the lowlands of southeastern China growing close to or at sea level in river deltas or other flooded areas (Flora of China Editorial Committee 1999) at an MAT of 14.5–26.6°C. *Glyptostrobus pensilis* (Staunton ex D. Don) K. Koch occurs in humid warm temperate climates [warmest month mean temperature (WMMT) >22°C], mostly with dry winter months (Cwa climate sensu Köppen) but occasionally (southeastern Sichuan) with no dry season (Cfa climate).

*Sequoia* constitutes coastal redwood forests in northern California and southern Oregon mainly below 300 m a. s. l. but occasionally reaching up to 1,000 m a. s. l.

(Flora of North America Editorial Committee 1993). Although its only modern representative *Sequoia sempervirens* (D. Don) Endl. is growing under a distinct Mediterranean macroclimate (Csa climate sensu Köppen) with winter rain and dry summer months, the actual climate resembles more a humid warm temperate Cfa/b climate because fog is acting as the main water source during the dry summer months (Dawson 1998). MAT in redwood forests ranges from 9.4°C to 15.3°C (Thompson et al. 1999a).

Among angiosperms, *Cercidiphyllum* is represented today by two species in China and Japan. *Cercidiphyllum japonicum* Sieb. and Zucc. is part of mixed mesophytic forests and deciduous broadleaved forests, often along streams and at forest margins, in northern parts of southeast China and in Japan. It occurs between 600 and 2,700 m a. s. l. with MAT between 2.6°C and 15.9°C. *Cercidiphyllum magnificum* (Nakai) Nakai is endemic to central and northern Honshu, Japan, growing in deciduous forests along streams (Iwatsuki et al. 2006) between 500 and 1,500 m a. s. l. (Ohwi 1965). The species thrives at MAT 4.6–11.6°C. Both species are growing under a Cfa/b climate.

*Fagus* consists of ten modern species in humid temperate areas of the northern hemisphere (Shen 1992; Denk 2003; Denk et al. 2005). *Fagus friedrichii* Grímsson & Denk belongs to an extinct Miocene lineage of *Fagus* extending from Alaska to Iceland (Grímsson and Denk 2005) and has been compared by the same authors to the modern North American *F. grandifolia* Ehrh. and the Japanese *F. crenata* Engl. A recent re-evaluation of this fossil species showed that it is most closely related among all modern and extinct species to *Fagus washoensis* LaMotte and *F. idahoensis* Axelrod & Chaney from the Miocene of western North America (Denk and Grimm 2009). Of the modern species comparable to *Fagus friedrichii*, *Fagus crenata* occurs from 5 to 1,500 (2,100) m a. s. l. At its northern distribution limit it forms forests close to sea level, while it covers a wide vertical range in its southern range (Shen 1992). It forms part of mixed broadleaved deciduous and conifer forests under a Cfa/b (to Dfa/b) climate, MAT 3–13°C (Peters 1997). *Fagus grandifolia* has a wide distribution in North America ranging from northern Florida to southern Canada and with a disjunct area in Mexico (Shen 1992). The American beech occurs in mixed woods, deciduous forests and mixed broadleaved and conifer forests ranging from sea level to 1,000 m a. s. l. (Flora of North America Editorial Committee 1997). It thrives in humid warm-temperate climates (Cfa/b to Dfa/b climate) with MAT 4–21°C (Peters 1997).

*Platanus* is a small northern hemispheric genus with seven species (Nixon and Poole 2003). The fossil species from Iceland compares well with the North American *P. occidentalis* L. *Platanus occidentalis* covers a range from eastern Canada to Texas and northern Mexico. It is commonly found in alluvial forests along streams and lakes, sometimes in ravines and on uplands, stretching from sea level to about 1,000 m a. s. l. (Flora of North America Editorial Committee 1997). While the species grows mainly under a humid Cfa climate, with a MAT ranging from 5.4°C to 21.1°C (Thompson et al. 1999b), it enters a small zone of dry steppe climates (BSk climate sensu Köppen) in its southwestern range. Here, it does not occur as part of extensive forests but is confined to riparian communities in depressed river valleys and moist ravines.

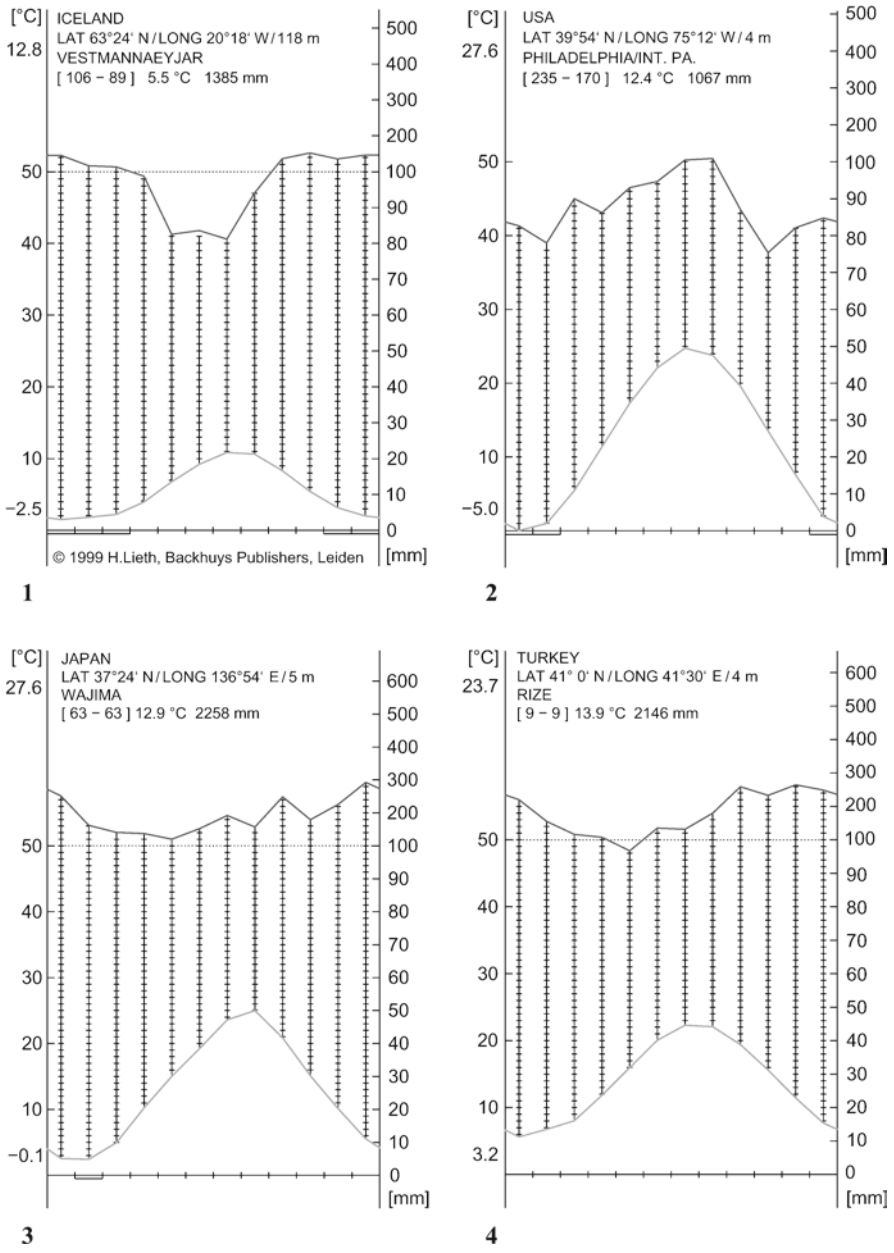



**Fig. 4.6** Climate diagrams for modern Iceland, and for climate stations resembling the climatic conditions inferred for the mid-Miocene of Iceland (Climate diagrams from Lieth et al. 1999). **1**. Vestmannaeyjar, Cfc climate. **2**. Philadelphia, Cfa climate. **3**. Wajima, Cfa climate. **4**. Rize, Cfa climate (Climate types according to Köppen, cf. Kottek et al. 2006)

Except for some few taxa that occur in a wide range of climatic types, e.g. *Juniperus* sp., most of the taxa recorded for the ca 15 Ma formation are typical components of forests thriving under a humid warm temperate climate without any dry season (Cfa including Submediterranean variants of Cfb climates). Cfa climates are currently found in the (south)eastern United States (roughly corresponding to the "Eastern Deciduous Forests" of North America; Braun 1950) and montane forests of eastern Mexico (Miranda and Sharp 1950). In western Eurasia, Cfa climates are restricted to southern Europe, the Balkans, and the areas along the eastern Black Sea (Euxinian forests) and southern Caspian Sea (Hyrcanian forests; Meusel et al. 1965; Denk 1998; Denk et al. 2001). In East Asia Cfa climates are found in southeast China and Japan (mixed mesophytic forests and mixed broadleaved deciduous and evergreen forests; Wang 1961; Wolfe 1979).

Although modern analogues of several taxa co-existing in Iceland ca 15 Ma currently display distribution ranges that do not overlap (for example, *Glyptostrobus* and *Sequoia*), they share a number of ecological and climatic features. Overall, they suggest that the Icelandic forests flourished under humid warm temperate climates (Cfa to Cfb climate).

The minimal temperature requirements (MAT) of the taxa encountered in the ca 15 Ma floras are between 8°C and 12°C for upland environments and up to ca 15°C for lowland riparian elements such as *Glyptostrobus*. The position of Iceland in the North Atlantic would suggest that rainfall was evenly distributed over the year as it is today (fully humid Cfc climate in coastal lowlands; Kottek et al. 2006). Climatic diagrams probably matching the conditions for Iceland ca 15 Ma are shown in Fig. 4.6.

## 4.5 Taxonomic Affinities and Origin of the Early Icelandic Floras

Many of the species encountered in the Middle Miocene of Iceland belong to genera that had a wide northern hemispheric distribution during that time; they could have reached Iceland either from North America or Eurasia. Examples include *Cathaya* (Liu and Basinger 2000; Saito et al. 2000; Hofmann et al. 2002), *Glyptostrobus* (Mai 1995; Budantsev 1997; Manchester 1999), *Sequoia* (Knobloch 1969; Meyer and Manchester 1997), *Cercidiphyllum* (La Motte 1936; Ferguson 1971; Shilin 1974; Ozaki 1991; Kovar-Eder et al. 2004). More detailed biogeographical analyses of these genera will depend on morphological studies evaluating transcontinental taxonomic relationships with higher taxonomic and stratigraphic resolution.

By contrast, a small number of the genera are believed to have had a narrower geographic distribution in the northern hemisphere, and hence provide more information regarding the migration routes to Iceland. *Cryptomeria* has a fossil record that dates back to the Paleocene in Europe (Mai 1995). Unambiguous macrofossils are not older than Miocene (Kilpper 1968; Boulter 1969; Boulter and Chaloner 1970; Dolezych and Schneider 2007). The genus is entirely absent from the fossil record of North America (Manchester 1999). In view of the fossil distribution and the present

range of the genus (endemic with a single species in Japan), *Cryptomeria* is a strict Eurasian element and must have migrated to Iceland from continental Europe.

Another interesting finding is that *Rhododendron* pollen recovered from the Langhian sediments of Iceland is indistinguishable from modern pollen of the western Eurasian species *R. ponticum* (Plate 4.11). The modern sister species of *R. ponticum*, the eastern North American *R. maximum*, is morphologically very similar to the Eurasian species but has a very distinct pattern of pollen tectum (Denk et al. unpublished data). This may indicate that *Rhododendron* migrated to Iceland from Europe during or before the early Middle Miocene.

*Fagus friedrichii* represents an extinct lineage within the genus *Fagus* (Grímsson and Denk 2005; Plate 4.12) and the fossil record suggests that it had a disjunct distribution between Alaska and Iceland during the Miocene. Foliage resembling *F. friedrichii* has never been reported from European sediments (Denk 2004; Grímsson and Denk 2005). Further, a recent re-evaluation of *F. friedrichii* showed that it is most closely related among all modern and extinct species to *Fagus washoensis* and *F. idahoensis* from the Miocene of western North America (Denk and Grimm 2009). The latter two fossil species should perhaps be treated as two morphotypes of a single species (Chaney and Axelrod 1959). This suggests that *Fagus friedrichii* or its ancestors migrated to Iceland from North America via Greenland and is in agreement with the palynological record of *Fagus* in eastern and Arctic North America during the Early and Middle Miocene (see below Sect. 4.6).

Recently, pollen, foliage, and fruits belonging to *Tetracentron* have been reported from Iceland (Grímsson et al. 2008). This finding is surprising because previously the genus was known only from East Asia and western North America (Suzuki 1967; Ozaki 1987; Chelebaeva and Shancer 1988; Manchester and Chen 2006; Pigg et al. 2007). The genus comprises a single living species, *T. sinense* Oliv., that occurs from central and southern China to northeastern India. The presence of *Tetracentron* in the Miocene of Iceland suggests that the biogeographic history of the genus is much more complex than previously thought. *Tetracentron* has very small pollen that is hard to discern in LM. A screening of European Neogene sediments for the genus using scanning electron microscopy (SEM) did not yield any *Tetracentron* pollen (Grímsson et al. 2008). Although more SEM studies are needed, this may indicate a migration to Iceland via Canada and Greenland similar to the *Fagus* pathway.

In summary, the distribution of closely related coeval fossil taxa provides convincing evidence that Iceland was colonized both from the east (Eurasia) and the west (North America/Greenland) in the Cainozoic.

## 4.6 Comparison to Coeval Northern Hemispheric Floras

Many well-studied Middle Miocene floras of the northern hemisphere are situated at lower latitudes than the floras from Selárdalur and Botn. During the Middle Miocene the thermal gradient from low to high latitudes was not as pronounced as

today and earliest signals of ice rafted debris in the northernmost North Atlantic are from 14 Ma (Thiede et al. 1998). Hence, mid and high latitude floras shared a number of warm temperate taxa such as *Aesculus*, *Carpinus*, *Platanus*, and *Pterocarya* (Table 4.3). Nevertheless, a latitudinal gradient in vegetation and climate can be expected. At present, the mid-Miocene floras from Iceland are situated close to the Arctic Circle (66°33′N).

**Table 4.3** Taxa of the 15 Ma floras from Iceland that are shared with some mid-Miocene floras of the northern hemisphere (Data from Tanai and Suzuki 1963; Christensen 1975, 1976, 1978; Wolfe and Tanai 1980; Koch 1984; Friis 1985; Gray 1985; Rember 1991; Liu and Leopold 1992; Liu et al. 1996; Kvaček and Rember 2000, 2007; Sun et al. 2002; Liang et al. 2003; Kovar-Eder et al. 2004)

| | 1 Søby | 2 Seldov | 3 Abura | 4 Clarkia | 5 Parsch | 6 Shanw |
|---|---|---|---|---|---|---|
| *Acer* | + | + | + | + | + | + |
| *Aesculus* | | | + | + | | + |
| *Alnus* | + | + | + | + | + | + |
| *Betula* | + | + | + | + | + | + |
| *Carpinus* | + | + | + | | | + |
| *Cathaya* | | | | | + | |
| *Cercidiphyllum* | | + | + | + | + | |
| ***Cryptomeria*** | | | | | | |
| *Fagus* | | + | + | + | + | + |
| *Glyptostrobus* | | + | + | + | + | |
| *Ilex* | + | | | + | | |
| ***Juniperus*** | | | | | | |
| Liliaceae | | ? | | | | |
| *Magnolia* | + | | + | + | | |
| *Parthenocissus* | | | | + | | |
| *Picea* | + | | + | + | | + |
| *Pinus* | + | | + | + | + | + |
| *Platanus* | + | + | | + | + | |
| Polypodiaceae | | | | + | | + |
| *Pterocarya* | + | | + | + | | + |
| *Rhododendron* | + | | | | | + |
| Rosaceae | | + | + | + | | + |
| *Salix* | + | + | | + | | + |
| *Sanguisorba* | | | | | | |
| *Sequoia* | + | | | + | | |
| ***Tetracentron*** | | | | | | |
| *Tilia* | | + | + | + | + | + |
| *Tsuga* | + | | + | + | | + |
| *Ulmus* | + | + | + | + | + | + |
| ***Viburnum*** | | | | | | |

Taxa in bold are recorded from Iceland only. *1* Søby flora, Denmark [56°21′N]; *2* Seldovian Point flora, Alaska [59°26′N]; *3* Abura flora, Hokkaido (Japan) [ca. 42°N]; *4* Clarkia flora, Idaho USA) [47°00′N]; *5* Parschlug flora, Austria [47°29′N]; *6* Shanwang flora, China [36°54′N]

In the following section, the Icelandic floras are compared to a number of northern hemisphere floras situated between 30°N and 60°N. Closest is the Seldovia Point flora from Alaska described by Heer (1869), Wolfe (1966), Wolfe et al. (1966), and Wolfe and Tanai (1980) at around 60°N. Compared to the Icelandic floras, the Seldovia Point flora is more diverse at the generic level (33 vs. 46 genera, Appendix 4.1), and based on the macrofossil record (according to the treatment of Wolfe and Tanai 1980), has some warm temperate/subtropical elements that are entirely absent from the Icelandic floras (*Alangium*, *Cladrastis*, *Cocculus*, Table 4.4;

**Table 4.4** Taxa missing from Iceland shared by two or more mid-Miocene floras located more southerly than Iceland (Data from Tanai and Suzuki 1963; Christensen 1975, 1976, 1978; Wolfe and Tanai 1980; Koch 1984; Friis 1985; Gray 1985; Rember 1991; Liu and Leopold 1992; Liu et al. 1996; Kvaček and Rember 2000, 2007; Sun et al. 2002; Liang et al. 2003; Kovar-Eder et al. 2004)

| | 1 Søby | 2 Seldov | 3 Abura | 4 Clarkia | 5 Parsch | 6 Shanw |
|---|---|---|---|---|---|---|
| *Ailanthus* (Simaroubaceae) | | | + | + | + | + |
| *Alangium* (Alangiaceae) | | + | | | | + |
| Anacardiaceae | | | | + | + | + |
| *Castanea* (Fagaceae) | + | | + | + | | + |
| *Celastrus* (Celastraceae) | | | | | + | + |
| *Celtis* (Celtidaceae) | | + | | + | + | + |
| *Cornus* (Cornaceae) | | | | + | + | + |
| *Diospyros* (Ebenaceae) | + | | | + | | + |
| *Engelhardia* Juglandaceae) | + | | | + | + | + |
| *Eucommia* (Eucommiaceae) | | + | | | | + |
| *Euonymus* (Celastraceae) | | | | | + | + |
| Fabaceae | + | + | + | + | + | + |
| Flacourtiaceae | + | | | | | + |
| *Fraxinus* (Oleaceae) | + | + | + | + | + | + |
| *Halesia* (Styracaceae) | + | | | + | | |
| *Hydrangea* (Hydrangeaceae) | | + | + | + | | + |
| *Kalopanax* (Araliaceae) | | + | | | | + |
| *Keteleeria* (Pinaceae) | | | + | + | | + |
| *Liquidambar* (Hamamelidaceae) | + | + | + | + | + | + |
| Menispermaceae | | + | + | | | |
| *Metasequoia* (Cupressaceae) | | + | + | + | | |
| Myricaceae | + | | | + | + | + |
| *Nyssa* (Nyssaceae) | + | + | | + | | + |
| *Ostrya* (Betulaceae) | | + | + | + | | + |
| *Paulownia* (Paulowniaceae) | | | | + | | + |
| Rhamnaceae | | | | + | + | + |
| *Symplocos* (Symplocaceae) | + | | | + | | |
| *Taxodium* (Cupressaceae) | + | | | + | | |
| Theaceae | | | + | | + | |
| *Vitis* (Vitaceae) | | + | | + | | + |
| *Zelkova* (Ulmaceae) | | + | + | + | + | + |

*1* Søby flora, Denmark [56°21′N]; *2* Seldovian Point flora, Alaska [59°26′N]; *3* Abura flora, Hokkaido (Japan) [ca. 42°N]; *4* Clarkia flora, Idaho USA) [47°00′N]; *5* Parschlug flora, Austria [47°29′N]; *6* Shanwang flora, China [36°54′N]

Appendix 4.1). Also lianas are more diverse in the Seldovia Point flora as compared to Iceland (three vs. one taxon). At the same time, the Icelandic floras appear to be much richer in conifers (eight vs. three taxa). Overall, the similarity between these two floras appears quite high; both represent mixed broadleaved deciduous and coniferous forests. Among the broadleaved deciduous elements *Acer*, Betulaceae, *Fagus*, and *Ulmus* are important (Table 4.3). Another mid-Miocene flora well comparable to the Icelandic floras is the Abura flora from Hokkaido, Japan (ca. 42°30′N; Tanai and Suzuki 1963). The Abura flora shares some taxa that are missing from Iceland with the Seldovia Point flora (*Hydrangea*, Menispermaceae) and with the much richer floras from Shanwang, China; Clarkia, Idaho, USA; and Parschlug, Austria (e.g., *Ailanthus,* Fabaceae*, Hydrangea*, Theaceae; see Table 4.4). At the same time, the high amount of broadleaved deciduous taxa, with *Acer*, Betulaceae, and *Ulmus* playing an important role, and several conifers is shared between the Abura and the Icelandic floras. The fact that the Abura flora is situated much more to the south than the Icelandic floras could reflect a northward shift of the temperate climate zone at the western margin of Eurasia already during the Middle Miocene. Today, temperate vegetation (Cfa and Cfb climates) extends much farther north along the western margin of Eurasia than along its eastern margin (Kottek et al. 2006); this anomaly is attributed to the warm Gulf Stream along the western margin of Eurasia.

In contrast, the Søby flora of Denmark (56°21′N; Christensen 1975, 1976, 1978; Koch 1984; Friis 1985) which is geographically closest to Iceland is more diverse than the Icelandic floras and shares a substantial number of elements that are absent from Iceland with mid latitude floras typically representing mixed mesophytic forests (e.g. Fabaceae, Flacourtiaceae, Nyssaceae, Styracaceae, and Symplocaceae; the latter three usually require taphonomic conditions of carpofloras for recognition, Appendix 4.1). For this reason, Mai (1995) included the Fasterholt-Søby floras within the Central European Middle Miocene mixed mesophytic forests and recognized that these floras represent the northernmost occurrences of the (humid warm temperate or subtropical) “Mastixioid floras” (Mai 1995, p. 369).

The North American Clarkia flora (47°00′N; Gray 1985; Rember 1991; Kvaček and Rember 2000, 2007) and the Central European Parschlug flora (47°29′N; Kovar-Eder et al. 2004) are markedly more diverse than the Icelandic flora. These two floras and the eastern Chinese Shanwang flora (36°54′N; Liu and Leopold 1992; Liu et al. 1996; Sun et al. 2002; Liang et al. 2003) are representing typical mixed mesophytic forests. They share a relatively large number of taxa not recorded from Iceland (Table 4.4). At the same time, the Clarkia flora has most taxa in common with the Icelandic flora (Table 4.3).

Manchester (1999) listed the geographic and stratigraphic distribution of selected conifer and angiosperm genera in the northern hemisphere. For the Miocene, 28 genera are shared between Europe and North America, of which ten genera are also found in Iceland (*Acer*, *Alnus*, *Betula*, *Cercidiphyllum*, *Comptonia*, *Fagus*, *Glyptostrobus*, *Liriodendron*, *Pterocarya*, and *Tilia*). All these genera, including members of the largely evergreen families Magnoliaceae (*Liriodendron*), Myricaceae (*Comptonia*), and the taxodiaceous genus *Glyptostrobus*, are deciduous. Among the taxa not present in Iceland, *Ailanthus, Hydrangea,*

*Gordonia, Liquidambar, Symplocos,* and the palm genus *Sabal* are typical (compare Manchester 1999 and Appendix 4.1).

In total, the mid-Miocene floras of Iceland show some overall similarities to a number of mid latitude floras from Eurasia and North America but lack typical thermophilic elements shared among most of the mid latitude floras (Table 4.4).

A number of taxa recorded from Iceland but absent from coeval floras of other regions may have occurred in these floras as well but have been overlooked due to their inconspicuous, small pollen (*Tetracentron*; cf. Grímsson et al. 2008), or misidentified in case of *Cathaya* (cf. Liu and Basinger 2000; Saito et al. 2000; Hofmann et al. 2002).

In addition, there is a noticeable similarity of the ca 15 Ma Icelandic floras with a number of Early to Middle Miocene floras from Arctic North America (situated well above 60°N; Matthews and Ovenden 1990; Fyles et al. 1994; White and Ager 1994) and, among others, the Early Miocene mid latitude flora from Brandon Lignite, eastern North America (Tiffney 1994; Traverse 1994; Table 4.5; Appendix 4.2).

Some of the Arctic North American floras are less suitable for comparison with Icelandic ca 15 Ma floras because they represent azonal wetlands and aquatic vegetation with large amounts of herbaceous plants (Ballast Brook Formation and Mary Sachs Gravels, Banks Island; West River, Horton River area, Northwest Territories; Table 4.5, Appendix 4.2). Fyles et al. (1994) suggested that the Middle Miocene Ballast Brook beds represent a cypress swamp type of environment. Taxa such as *Liriodendron*, *Comptonia*, and *Decodon* recorded in these floras occur in younger Icelandic floras (see Chaps. 5, 6). In contrast, Whitlock and Dawson (1990) reported a palynoflora from the Early Miocene Haughton Formation from Devon Island at about 75°N that resembles more the floras of Iceland (Table 4.5). These authors interpreted some of the pollen and spores as reworked from older sediments (e.g. *Gleichenidites*). Furthermore, based on the absence in the macroflora, they assumed single pollen grains of *Liquidambar*, *Castanea*, *Platanus*, and *Ilex* to be derived from distant (more southerly) sources. From Devon Island, the only early Neogene vertebrate remains from Arctic North America have been recovered: two salmoniform fishes (trout, *Eosalmo* sp., and a smelt-like fish, cf. *Osmerus* sp.), one swan (tribe *Cygnini*), and four representatives of mammals (a shrew, family Soricidae, subfamily Heterosoricinae, cf. *Domnina* sp., a rabbit, family Leporidae, similar to some North American species referred to the extinct genus *Desmatolagus*, a rhinoceros, and a specimen of uncertain affinity; Whitlock and Dawson 1990). A Dfa to Dfb climate has been inferred for the Haughton Formation but the interpretation of both the plant and animal record remains rather unsatisfying. The closest match to the Middle Miocene floras of Iceland is seen in the flora of the Upper Rampart Canyon of the Porcupine River in central Alaska (White and Ager 1994; Table 4.5, Appendix 4.2). This flora is situated at approximately the same latitude as the Icelandic floras and radiometrically dated to 15.2 ± 0.1 Ma. Owing to the absence of a topographic barrier between central Alaska and the Pacific, the climate was oceanic and favoured a type of vegetation similar to the one from Iceland. Today, the Rampart Canyon is exposed to a cold continental Dsc

**Table 4.5** Taxa shared between the mid-Miocene floras of Iceland and Early to Middle Miocene floras from Arctic and temperate North America (Data from Matthews and Ovenden 1990; Whitlock and Dawson 1990; Fyles et al. 1994; White and Ager 1994)

| | 1 Porcupine | 2 Ballast | 3 West R. | 4 Mary S. | 5 Haughton | 6 Brandon |
|---|---|---|---|---|---|---|
| *Acer* | + | | | | + | |
| ***Aesculus*** | | | | | | |
| *Alnus* | + | + | | + | + | |
| *Betula* | + | + | + | + | + | |
| *Carpinus* | + | | | | + | |
| *Cathaya* | | | | | | +[a] |
| *Cercidiphyllum* | + | | | | | |
| ***Cryptomeria*** | | | | | | |
| *Fagus* | + | | | | + | + |
| *Glyptostrobus* | | + | | + | | + |
| *Ilex* | + | | | | [+] | + |
| *Juniperus* | | + | | | | |
| **Liliaceae** | | | | | | |
| *Magnolia* | | | | | | + |
| *Parthenocissus* | | | | | | + |
| *Picea* | + | + | + | + | + | |
| *Pinus* | + | + | | + | + | + |
| ***Platanus*** | | | | | | |
| Polypodiaceae | + | | | | | |
| *Pterocarya* | + | | | | + | + |
| *Rhododendron* | | | | | | + |
| Rosaceae | | | | | | + |
| *Salix* | + | + | | | + | |
| ***Sanguisorba*** | | | | | | |
| *Sequoia* | + | | | | | |
| ***Tetracentron*** | | | | | | |
| *Tilia* | + | | | | | + |
| *Tsuga* | + | + | + | | + | |
| *Ulmus* | + | | | | + | + |
| ***Viburnum*** | | | | | | |

Taxa in bold are recorded from Iceland only. *1* Porcupine River, C Alaska [67°20′N, 142°20′W], Middle Miocene; *2* Ballast Brook Formation, Banks Island [74°20′N, 123°15′W], Middle Miocene; *3* West River, Horton River area, N. W. Territories [69°12′N, 127°02′W], late Early Miocene; *4* Duck Hawk Bluffs, Mary Sachs gravels, Banks Island [71°57′N], late Early Miocene; *5* Haughton Formation, Devon Island [75°22′N, 89°40′W], Early Miocene; *6* Brandon Lignite, Vermont [43°50′N, 73°03′W], Early Miocene

[a]As *Abietineaepollenites baileyanus* (Traverse) Zhu, *A. microalatus* Potonié, and *Pinuspollenites tenuextimus* (Traverse) Traverse

climate sensu Köppen with a MAT of −8.6°C (as compared to the Cfc climate with MAT 5.5°C for the Vestmannaeyjar Islands in the south of Iceland; Fig. 4.6). For the richest plant bearing layer (organic bed 3) yielding thermophilous woody angiosperms such as *Fagus*, *Quercus*, *Carya*, *Carpinus*, *Castanea*-type, *Ceridiphyllum*, *Juglans*, *Liquidambar*, cf. *Nyssa*, *Tilia*-type, and *Ulmus*-type, White and Ager

(1994) suggest a MAT of 9–10°C or even warmer. The modern analogue for this flora would be in the warm range of the "Mixed Northern Hardwood Forest" sensu Wolfe (1979), or the cool range of the "Mixed Mesophytic Forest" sensu Wolfe.

Finally, the Early Miocene flora of Brandon Lignite, Vermont, eastern North America (Tiffney 1994; Traverse 1994; Graham 1999), provides an example for a flora that may in part have acted as source vegetation for Arctic floras from Alaska to Devon Island and Iceland (Appendix 4.2). Taxa shared between the Brandon Lignite and 15–12 Ma floras from Iceland are, among others, *Cathaya*, *Corylus*, *Fagus*, *Magnolia*, *Parthenocissus*, *Pterocarya*, *Rhododendron*, and *Tilia*. Western North American Miocene floras may have acted as source vegetation as well (cf. Seldovia Point Flora, Table 4.3, Appendix 4.1, or the Miocene floras from the Columbia Plateau, Oregon, described by Chaney and Axelrod 1959). *Fagus idahoensis* and *F. washoensis* from the Columbia Plateau resemble most closely *F. friedrichii* from Alaska and Iceland (Grímsson and Denk 2005; Denk and Grimm 2009). The presence of *Fagus* in Miocene sediments from western North America, western Alaska, central Alaska, and Banks Island, may point to a possible pathway for *Fagus* to Iceland via Greenland (although Miocene plant bearing sediments are lacking from Greenland).

## 4.7 Early Colonization of Iceland

From the foregoing, we can proceed to consider scenarios for the early colonization of Iceland. In view of the traditional notion that Iceland was an isolated island by the Middle Miocene (Nilsen 1978; McKenna 1983a, b) we need to assess how an early colonization of Iceland would physically have been achievable. Evaluating the dispersal mechanisms of all the taxa shows that at least some (*Aesculus, Fagus*) could not have possibly colonized Iceland crossing large ocean barriers. Furthermore, most anemochorous taxa recorded have a very limited dispersal radius (*Cathaya, Glyptostrobus, Acer, Carpinus, Cercidiphyllum, Fraxinus*, *Platanus*, *Tetracentron, Tilia, Ulmus*; cf. Ridley 1930; van der Pijl 1982; Grímsson and Denk 2007).

Generally, only a few taxa from the ca 15 Ma formation have dispersal modes conducive to transport over long distances (*Betula*, *Salix, Rhododendron*). The remaining taxa are dispersed by animals over short distances (*Fagus*, *Aesculus*; mammals) or long distances in various ways (*Ilex, Lonicera, Magnolia,* and *Parthenocissus* by birds, endozoochory; *Platanus* by mammals or birds, exozoochory). This suggests that when proto-Iceland was colonized, it was connected to the mainland or accessible via a chain of islands. This land was part of the Greenland-Scotland Transverse Ridge that persisted from the early Cainozoic into the Miocene (Poore 2008; see Chap. 12 for a more comprehensive discussion).

The oldest exposed volcanic rocks on Iceland are ca 16 Ma. The sediments containing the oldest floras are approximately 15 Ma (McDougall et al. 1984; Hardarson et al. 1997; Kristjansson et al. 2003). Interestingly, a considerable number of the genera (*Glyptostrobus, Aesculus, Platanus, Ulmus, Magnolia* etc.) had

also been present in the older Brito-Arctic Igneous Province (BIP) floras (Spitsbergen; Heer 1883; Schloemer-Jäger 1958; Greenland; Koch 1963; Scotland; Boulter and Kvaček 1989), although these floras are at least 20 million years older. Considering a subaerial Greenland-Scotland Transverse Ridge (including proto-Iceland) long before 16 Ma (Poore 2008; see Fig. 12.2, Chap. 12), it is most likely that some of the species from the oldest floras migrated to proto-Iceland prior to the Middle Miocene and persisted until the accumulation of the ca 15 Ma sedimentary rock formation. The taxa recorded in the oldest sedimentary rocks in Iceland may have different geographical and temporal origins. Fossils similar to *Aesculus* and *Cercidiphyllum* recorded from Iceland were elements of the Palaeogene BIP floras and might have persisted in this area over a long time. In contrast, *Fagus friedrichii* with clear biogeographic affinities to Alaska, most likely colonized Iceland in the course of the Middle Miocene via North America and Greenland (Denk and Grimm 2009).

## 4.8 Summary

In this chapter the floristic composition and palaeoecology of the oldest floras from Iceland are reviewed. Although the Middle Miocene floras from Iceland are not as rich in species as co-eval mid latitude floras, they point to the presence of warm temperate broad leaved deciduous and evergreen forest with a strong component of conifers in Iceland during the Langhian stage. The temperature requirements (MAT) of the taxa recorded are between 8°C and 12°C for upland environments and up to 15°C for lowland riparian elements. Furthermore, the position of Iceland in the North Atlantic would suggest that rainfall was evenly distributed over the year as it is today (Cf climate type sensu Köppen). A taxonomic evaluation of Icelandic fossils and comparable modern and fossil taxa suggests that at least some taxa reached Iceland from Eurasia (*Cryptomeria* and *Rhododendron ponticum* type), whereas others migrated from North America (*Fagus friedrichii* and *Tetracentron atlanticum*). The presence of chiefly dyschorous taxa (*Aesculus, Fagus*) and anemochorous taxa with short dispersal radii (*Cathaya, Glyptostrobus, Acer, Carpinus, Cercidiphyllum, Fraxinus*, *Platanus*, *Tetracentron, Tilia, Ulmus*) points to the presence of a physical link between both North America-Greenland and Iceland, and Europe and Iceland during the time at which proto-Iceland was colonized.

## Appendix 4.1

Floristic composition of the 15 Ma sedimentary formation of Iceland compared to contemporaneous northern hemispheric fossil assemblages at latitudes below 60°N (Floral lists from Tanai and Suzuki 1963; Wolfe and Tanai 1980; Gray 1985; Rember 1991; Liu and Leopold 1992; Liu et al. 1996; Kvaček and Rember 2000, 2007; Sun et al. 2002; Liang et al. 2003; Kovar-Eder et al. 2004).

| **Selárdalur-Botn flora, Iceland [65°46′N]** 15 Ma This study | |
|---|---|
| 1 | Polypodium sp. |
| 1 | Polypodiaceae gen. et spec. indet. 1 |
| 1 | Cathaya sp. |
| 1 | Cryptomeria sp. |
| 1, 2 | Glyptostrobus europaeus |
| 1 | Juniperus sp. |
| 2 | ?Picea sp |
| 1 | Pinus sp. 1 Diploxylon |
| 1, 3 | Sequoia abietina |
| 1 | Tsuga sp. |
| 1 | Acer sp. 1 (Sect. Acer) |
| 1 | Acer sp. 2 |
| 2 | Aesculus sp. |
| 1 | Alnus sp. 1 |
| 1 | Betula sp. 1 |
| 1 | Carpinus sp. 1 |
| 1, 3 | Cercidiphyllum sp. |
| 1, 2 | Fagus friedrichii |
| 1 | Ilex sp. 1 |
| 3 | Lonicera sp. |
| 1 | Liliaceae gen. et spec. indet. 1 |
| 2 | cf. Magnolia sp. |
| 1 | Parthenocissus sp. [L] |
| 1, 3 | Platanus leucophylla |
| 1 | Pterocarya sp. |
| 1, 3 | Rhododendron sp. 1 |
| 1 | Rosaceae gen et. spec. indet. 1 |
| 1 | Rosaceae get et spec. indet. 2 |
| 1 | Rosaceae get et. spec. indet. 3 |
| 1 | Salix sp. 1 |
| 1 | Sanguisorba sp. |
| 1 | Tetracentron atlanticum |
| 1, 3 | Tilia selardalense |
| 1, 3 | Ulmus sp. MT1 |
| 1 | Viburnum sp. |

| **Søby flora, Denmark [56°21′N]** Pre Late Badenian (Langhian) Koch 1984 [1]; Friis 1985 [2]; Christensen 1975, 1976, 1978 [3] | |
|---|---|
| 1 | Abietinaepollenites microalatus |
| 1 | **Piceapollenites alatus** |
| 1, 2 | **Pinus thomasiana** |
| 1 | Sciadopityspollenites serratus |
| 1 | **Sequoiapollenites polyformosus** |
| 2 | Taxodium dubium |
| 1 | Taxodiaceaepollenites hiatus |
| 1 | **Tsugaepollenites sp.** |
| 2 | Hellia (Tetraclinis) salicornioides |
| 3 | **Acer soebyensis** |
| 2 | Alismataceae |
| 1 | **Alnipollenites versus** |
| 2 | Carex sp. 2 |
| 2 | Carex sp. 3 |
| 1 | Caryapollenites simplex |
| 3 | Castanea atavia |
| 2 | Cephalanthus pusillus |
| 2 | Cladiocarya europaea |
| 2 | Cladiocarya trebovensis |
| 3 | Comptonia acutiloba |
| 2 | Comptonia srodoniowae |
| 1 | Cyrillaceaepollenites megaexactus |
| 1 | Cyrillaceaepollenites exactus |
| 3 | Diospyros brachysepala |
| 2 | Dulichium marginatum |
| 1 | Engelhardtioipollenites spp. |
| 1 | Ericipites sp. |
| 3 | Fraxinus cf. ungeri |
| 2 | Halesia crassa |
| 2 | Hypericum danicum |
| 1 | **Ilexpollenites iliacus** |
| 3 | Juglans acuminata |
| 3 | Juglans juglandiformis |
| 2 | Leguminocarpon sp. |

(continued)

**Søby flora, Denmark** (continued)

| | |
|---|---|
| 1, 3 | Liquidambar europaea |
| 2 | Ludwigia corneri |
| 2 | Lysimachia sp. |
| 3 | **Magnolia sp.** |
| 2 | Microdiptera sp. |
| 1, 2 | Myrica sp. |
| 1 | Nyssapollenites sp. |
| 1, 2 | **Platanus neptunii** |
| 2 | Poliothyrsis eurorimosa |
| 1 | Polyporopollenites carpinoides |
| 2 | Potamogeton heinkei |
| 2 | Proserpinaca brevicarpa |
| 1 | **Pterocaryapollenites stellatus** |
| 1 | Quercoidites henrici |
| 1 | Quercoidites microhenrici |
| 1 | Rhoipites pseudocingulum |
| 3 | **Salix lavateri** |
| 1 | Sapotaceoidaepollenites sp. |
| 2 | Saururus bilobatus |
| 2 | Scirpus ragozinii |
| 1, 3 | Smilax weberi |
| 1, 2 | Symplocos gothanii |
| 2 | Teucrium sp. 2 |
| 1 | Triporopollenites coryloides |
| 1 | **Trivestibulopollenites betuloides** |
| 1, 3 | **Ulmus pyramidalis** |

**Seldovian Point flora, Alaska [59°26′N]**
Late Early to early Middle Miocene
Wolfe and Tanai 1980

| | |
|---|---|
| 3 | Dryopteris sp. |
| 3 | Onoclea sensibilis |
| 3 | **Glyptostrobus europaeus** |
| 3 | Ginkgo biloba |
| 3 | **Acer ezoanum Oishi & Huzioka** |
| 3 | **Acer glabroides** |
| 3 | **Acer grahamensis** |
| 3 | **Acer heterodentatum** |
| 3 | Alangium mikii |
| 3 | Alisma seldoviana |
| 3 | **Alnus cappsi** |
| 3 | **Alnus fairi** |
| 3 | **Alnus healyensis** |
| 3 | **Betula cf. sublutea** |
| 3 | **Carpinus seldoviana** |
| 3 | Carya bendirei |
| 3 | Celtis sp. |
| 3 | **Cercidiphyllum alaskanum** |
| 3 | Cladrastis cf. aniensis |
| 3 | Cocculus auriculata |
| 3 | Corylus sp. |
| 3 | Crataegus chamisonii |
| 3 | Cyclocarya ezoana |
| 3 | Decodon alaskana |
| 3 | Eucommia cf. Montana |
| 3 | **Fagus aff. crenata** |
| 3 | **Fagus antipofi** |
| 3 | **Fraxinus kenaica** |
| 3 | Hemitrapa borealis |
| 3 | Hydrangea sp. |
| 3 | Kalopanax acerifolium |
| 3 | Liquidambar pachyphylla |
| 3 | Lonicera sp. |
| 3 | Monocotylophyllum alaskanum |
| 3 | Monocotylophyllum spp. |
| 3 | Nymphar ebae |
| 3 | Nyssa cf. knowltoni |
| 3 | Ostrya cf. oregoniana |
| 3 | **Platanus bendirei** |
| 3 | Populus kenaiana |
| 3 | Populus sp. |
| 3 | Potamogeton alaskanus |
| 3 | Prunus aff. padus |
| 3 | Prunus kenaica |
| 3 | **Pterocarya nigella** |
| 3 | Pueraria miothunbergiana |
| 3 | Quercus furuhjelmi |
| 3 | **Salix cappsensis** |
| 3 | **Salix hopkinsi** |
| 3 | **Salix picroides** |
| 3 | **Salix seldoviana** |
| 3 | Sorbaria hopkinsi |
| 3 | **Tilia subnobilis** |
| 3 | **Ulmus knowltoni** |
| 3 | **Ulmus owyheensis** |
| 3 | **Ulmus sp.** |
| 3 | **Ulmus speciosa** |
| 3 | Vitis seldoviana |
| 3 | Zelkova brownii |
| 3 | Zelkova ungeri |

**Abura flora, Hokkaido (Japan) [ca. 42° N]**
Middle Miocene Tanai and Suzuki 1963

| | |
|---|---|
| 3 | Abies aburaensis |
| 3 | Abies n-suzukii |
| 3 | **Glyptostrobus europaeus** |
| 3 | Keteleeria ezoana |
| 3 | Metasequoia occidentalis |
| 3 | **Picea hyamensis** |
| 3 | **Picea kaneharai** |
| 3 | **Picea kanoi** |
| 3 | **Picea magna** |
| 3 | **Picea ugoana** |
| 3 | **Pinus miocenica** |
| 3 | Pseudotsuga ezoana |
| 3 | Thuja nipponica |
| 3 | **Tsuga aburaensis** |
| 3 | **Tsuga miocenica** |
| 3 | **Acer ezoanum** |
| 3 | **Acer fatsiaefolia** |
| 3 | **Acer megasamarum** |
| 3 | **Acer miohenryi** |
| 3 | **Acer palaeodiabolicm** |
| 3 | **Acer protojaponicum** |
| 3 | **Acer prototataricum** |
| 3 | **Acer pseudoginnala** |
| 3 | **Acer subpictum** |
| 3 | **Aesculus majus** |
| 3 | Ailanthus yezoense |
| 3 | **Alnus miojaponica** |
| 3 | **Alnus protomaximowiczii** |
| 3 | **Betula sublutea** |
| 3 | Camellia protojaponica |
| 3 | **Carpinus miofangiana** |
| 3 | **Carpinus subcordata** |
| 3 | **Carpinus subyedoensis** |
| 3 | Carya miocathayensis |
| 3 | Castanea miomollissima |
| 3 | **Cercidiphyllum crenatum** |
| 3 | Comptonia naumanni |
| 3 | Corylus macquarrii |
| 3 | **Fagus antipofi** |
| 3 | Fraxinus wakamatsuensis |
| 3 | Hemitrapa borealis |
| 3 | Hydrangea lanceolimba |
| 3 | Juglans shanwangensis |
| 3 | Liquidambar miosinica |
| 3 | **Magnolia miocenica** |
| 3 | Menispermum sp. |
| 3 | Ostrya shiragiana |
| 3 | Populus nipponica |
| 3 | Populus reniformis |
| 3 | **Pterocarya ezoana** |
| 3 | Robinia nipponica |
| 3 | Rosa usyuensis |
| 3 | Sassafras subtriloba |
| 3 | **Tilia protojaponica** |
| 3 | **Ulmus longifolia** |
| 3 | **Ulmus shiragica** |
| 3 | Zelkova ungeri |

**Clarkia flora, Idaho (USA) [47°00′N]**
Middle Miocene Gray 1985 [1];
Rember 1991; Kvaček & Rember 2000, 2007 [3]

| | |
|---|---|
| 1 | Lycopodium sp. |
| 1 | Isoetes sp. |
| 1 | Osmunda sp. |
| 1 | **Polypodium vulgare type** |
| 1, 3 | Abies chaneyi |
| 3 | Amentotaxus californica |
| 3 | Calocedrus masonii |
| 1 | Cedrus sp. |
| 3 | Cephalotaxus sp. |
| 3 | Chamaecyparis linguaefolia |
| 3 | Cunninghamia chaneyi |
| 1 | Ephedra sp. |
| 3 | **Glyptostrobus oregonensis** |
| 3 | Keteleeria heterophylloides |
| 3 | Metasequoia occidentalis |
| 1, 3 | **Picea sp.** |
| 1, 3 | **Pinus harneyana** |
| 1, 3 | **Pinus tiptonia** |
| 1, 3 | **Pinus wheeleri** |
| 1 | Pseudotsuga |
| 3 | **Sequoia affinis** |
| 1 | Taxaceae-Cupressaceae-Taxaceae unspecified |
| 3 | Taxodium dubium |
| 3 | Taxus sp. |
| 3 | Thuja gracilis |
| 1 | Tsuga heterophylla |
| 1, 3 | **Acer cf. macrophyllum** |
| 1, 3 | **Acer cf. pensylvanicum** |
| 1, 3 | **Acer chaneyi** |
| 1, 3 | **Aesculus sp.** |
| 3 | Ailanthus sp. |
| 1, 3 | **Alnus relatus** |
| 3 | Amelanchier coveus |
| 1, 3 | **Betula fairii** |
| 1, 3 | **Betula vera** |

(continued)

**Clarkia flora, Idaho (USA)** (continued)

| | |
|---|---|
| 1 | Carya sp. |
| 3 | Caesalpinia spokanensis |
| 1, 3 | Castanea spokanensis |
| 1 | Celtis sp. |
| 3 | **Cercidiphyllum crenatum** |
| 1 | Chenopodiaceae gen. et spec. indet. |
| 3 | Cornus latahensis |
| 1 | Corylus sp. |
| 3 | Crataegus gracilens |
| 1 | Cyperaceae |
| 3 | Diospyros oregoniana |
| 1 | Engelhardia sp. |
| 1 | Ericaceae gen. et spec. indet. |
| 1, 3 | **Fagus idahoensis** |
| 1, 3 | Fraxinus sp. |
| 3 | Gleditsia sp. |
| 3 | Gordonia idahoensis |
| 1 | Gramineae |
| 3 | Gymnocladus sp. |
| 3 | Halesia/Symplocos |
| 3 | Heterosmilax sp. [L] |
| 3 | Hydrangea sp. |
| 1, 3 | **Ilex sinuata** |
| 1, 3 | Juglans lacunosa |
| 3 | Lauraceae gen. et sp. Indet. |
| 3 | Lindera oregoniana |
| 1, 3 | Liquidambar pachyphyllum |
| 1, 3 | Liriodendron Hesperia |
| 3 | Lithocarpus simulata |
| 1, 3 | **Magnolia cf. acuminata** |
| 1, 3 | **Magnolia dayana** |
| 3 | Morus sp. |
| 1 | Myrica |
| 3 | Nuphar sp. |
| 1, 3 | Nyssa copiana |
| 1, 3 | Nyssa hesperia |
| 1, 3 | Ostrya oregonia |
| 3 | Palaeocarya olsoni |
| 3 | Paliurus hesperius |
| 3 | Paulownia Columbiana |
| 3 | Persea pseudocarolinensis |
| 1 | Parthenocissus sp. |
| 3 | Philadelphus sp. |
| 1, 3 | **Platanus dissecta** |
| 3 | Populus lindgreni |
| 3 | Prunus sp. |
| 3 | Pseudofagus idahoensis |
| 1, 3 | Pterocarya mixta |
| 1, 3 | Quercus payettensis |
| 1, 3 | Rhamnus sp. |
| 1, 3 | Rhus sp. |
| 3 | Ribes sp. |
| 1 | **Rosaceae gen. et spec. indet.** |
| 3 | Salix hesperia |
| 3 | Sassafras columbiana |
| 1 | Shepherdia sp. |
| 3 | Smilax sp. [L] |
| 1 | Symplocos sp.? |
| 1 | **Tilia sp.** |
| 1, 3 | Typha sp. |
| 1, 3 | **Ulmus sp.** |
| 3 | Vaccinium sp. |
| 1, 3 | Vitis sp. [L] |
| 1, 3 | Zelkova oregonia |
| 3 | Zizyphoides-Nordenskioldia |

**Parschlug flora, Austria [47°29′N]**
Late Early to early Middle Miocene
Kovar-Eder et al. 2004

| | |
|---|---|
| 3 | Adiantum renatum |
| 3 | Osmunda parschlugiana |
| 3 | Pronephrium stiriacum |
| 3 | Salvinia cf. mildeana |
| 3 | ? **Cathaya sp**. |
| 3 | ? Cupressus sp. |
| 3 | **Glyptostrobus europaeus** |
| 3 | **Pinus spp. div.** |
| 3 | “Acacia” parschlugiana |
| 3 | “Celastrus” europaea |
| 3 | “Cornus” ferox |
| 3 | “Evonymus” latoniae |
| 3 | “Juglans” parschlugiana |
| 3 | “Quercus” daphnes |
| 3 | ? Chaneya sp. |
| 3 | ? Prinsepia sp. |
| 3 | **Acer integrilobum** |
| 3 | **Acer pseudomonspessulanum** |
| 3 | **Acer sp.** |
| 3 | **Acer tricuspidatum** |
| 3 | Ailanthus confucii |
| 3 | Ailanthus pythii |
| 3 | **Alnus gaudinii** |
| 3 | **Alnus julianiformis** |
| 3 | Antholithes stiriacus |
| 3 | Berberis (?) ambigua |
| 3 | Berberis teutonica |
| 3 | Berchemia multinervis |

(continued)

**Parschlug flora, Austria** (continued)

| | |
|---|---|
| 3 | **Betula cf. dryadum** |
| 3 | Buxus cf. egeriana |
| 3 | Cedrelospermum stiriacum |
| 3 | Cedrelospermum ulmifolium |
| 3 | Celtis japeti |
| 3 | **Cercidiphyllum crenatum** |
| 3 | cf. ? Gordonia oberdorfensis |
| 3 | cf. Rosa sp. |
| 3 | Cotinus (?) aizoon |
| 3 | Craigia bronnii |
| 3 | Cypselites sp. |
| 3 | Daphnogene polymorpha |
| 3 | Dicotylophyllum sp. 1 - 6 |
| 3 | Engelhardia macroptera |
| 3 | Engelhardia orsbergensis |
| 3 | **Fagus sp.** |
| 3 | Fraxinus primigenia |
| 3 | Leguminosites dionysi |
| 3 | Leguminosites hesperidum |
| 3 | Leguminosites palaeogaeus |
| 3 | Leguminosites parschlugianus |
| 3 | Liquidambar europaea |
| 3 | Liquidambar sp. |
| 3 | Mahonia (?) aspera |
| 3 | Monocotyledoneae gen. et sp. indet. |
| 3 | Myrica lignitum |
| 3 | Myrica oehningensis |
| 3 | Myrica sp. |
| 3 | Nerium sp. |
| 3 | Paliurus favonii |
| 3 | Paliurus tiliifolius |
| 3 | Phaseolites securidacus |
| 3 | **Platanus leucophylla** |
| 3 | Podocarpium podocarpum |
| 3 | Populus populina |
| 3 | Populus sp. |
| 3 | Prinsepia serra |
| 3 | Quercus drymeja |
| 3 | Quercus mediterranea |
| 3 | Quercus zoroastri |
| 3 | Saportaspermum sp. |
| 3 | Smilax sagittifera |
| 3 | Ternstroemites pereger |
| 3 | **Tilia longebracteata** |
| 3 | Toxicodendron herthae |
| 3 | **Ulmus parschlugiana** |
| 3 | **Ulmus plurinervia** |
| 3 | Zelkova zelkovifolia |

**Shanwang flora, China [36°54′N]**
Late Early to early Middle Miocene
Liu & Leopold 1992 [1]; Liu et al. 1996 [2]; Sun et al. 2002 [3]; Liang et al. 2003 [1]

| | |
|---|---|
| 1 | Osmunda sp. |
| 1 | **Polypodium type** |
| 2 | Pteris sp. |
| 1, 2 | Keteleeria ezoana |
| 1 | Larix/Pseudotsuga |
| 1 | **Picea type 1** |
| 1 | **Picea type 2** |
| 1 | **Pinus spp.** |
| 1 | **Tsuga sp.** |
| 1 | Taxodiaceae gen. et spec. indet. |
| 1 | Ephedra sp. |
| 1, 2 | **Acer diabolicum** |
| 1, 2 | **Acer florinii** |
| 1, 2 | **Acer miocaudatum** |
| 1, 2 | **Acer miodavidii** |
| 1, 2 | **Acer miohenryi** |
| 1, 2 | **Acer nordenskioldi** |
| 1, 2 | **Acer subpictum** |
| 1, 2 | **Acer trifoliatum** |
| 1 | Adenophera type |
| 2 | **Aesculus miochinensis** |
| 2 | Ailanthus youngii |
| 1 | Alangium sp. |
| 2 | Albizia miokalkora |
| 1, 2 | **Alnus prenepalensis** |
| 1, 2 | **Alnus protomaximowiczii** |
| 1 | Altingia sp. |
| 2 | Amelanchier sibirica |
| 2 | Ampelopsis shanwangensis |
| 2 | Aphananthe mioaspera |
| 2 | Astronium truncatum |
| 2 | Berchemia miofloribunda |
| 1, 2 | **Betula mioluminifera** |
| 1, 2 | **Carpinus cf. miofangiana** |
| 1, 2 | **Carpinus chaneyi** |
| 1, 2 | **Carpinus megabracteata** |
| 1, 2 | **Carpinus miocenica** |
| 1, 2 | **Carpinus mioturczaninowii** |
| 1, 2 | **Carpinus oblongibracteata** |
| 1, 2 | **Carpinus shanwangensis** |
| 1, 2 | **Carpinus subcordata** |
| 2 | Carrierea calycina |
| 1, 2 | Carya miocathayensis |
| 1 | Caryophyllaceae sp. |
| 2 | Cercis miochinensis |

(continued)

| | **Shanwang flora, China** (continued) |
|---|---|
| 2 | Castanea miomollissima |
| 1 | Castanopsis/Castanea sp. |
| 2 | Catalpa szei |
| 2 | Celastrus mioangulatus |
| 1, 2 | Celtis angusta |
| 1, 2 | Celtis bungeana |
| 2 | Ceratophyllum miodemersum |
| 2 | Chukrasia subtabularis |
| 2 | Cinnamomum oguniense |
| 2 | Commersonia parabatramia |
| 2 | Cornus miowalteri |
| 1, 2 | Corylus macquarrii |
| 2 | Cotoneaster protozabelii |
| 2 | Crataegus miocuneata |
| 2 | Cyperacites sp. |
| 2 | Diospyros miokaki |
| 1 | Engelhardia sp. |
| 2 | Eriobotrya miojaponica |
| 1, 3 | Eucommia sp. |
| 2 | Euodia miosinica |
| 2 | Euonymus protobungeanus |
| 1 | **Fagus sp.** |
| 2 | Ficus longipedia |
| 2 | Ficus shanwangensis |
| 2 | Firmiana sinomiocenica |
| 2 | Fraxinus dayana |
| 2 | Fraxinus microcarpa |
| 2 | Gleditsia miosinensis |
| 2 | Graminites sp. |
| 2 | Gymnocladus miochinensis |
| 2 | Hamamelis miomollis |
| 2 | Hovenia miodulcis |
| 2 | Hydrangea lanceolimba |
| 2 | Indigofera cf. pseudotinctoria |
| 1, 2 | Juglans acuminata |
| 1, 2 | Juglans miocathayensis |
| 1, 2 | Juglans shanwangensis |
| 2 | Kalopanax acerifolium |
| 2 | Koelreuteria macrocarpa |
| 2 | Koelreuteria miointegrifolia |
| 1 | **Ilex sp.** |
| 2 | Lindera paraobtusiloba |
| 2 | Lindera shanwangensis |
| 2 | Litsea grabaui |
| 1, 2 | Liquidambar miosinica |
| 1, 2 | **Lonicera cf. japonica** |
| 1, 2 | **Lonicera hispida** |
| 1, 2 | **Magnolia miocenica** |
| 2 | Mallotus populifolia |
| 2 | Malus parahupehensis |
| 1 | Melia sp. |
| 2 | Meliosma obtusifolia |
| 2 | Meliosma shanwangensis |
| 1 | Myrica sp. |
| 1 | Nyssa sp. |
| 1 | Oleaceae gen. et spec. indet. |
| 1, 2 | Ostrya uttoensis |
| 2 | Paliurus miosinicus |
| 2 | Paulownia shanwangensis |
| 2 | Phellodendron megaphyllum |
| 2 | Physocarpus shandongensis |
| 2 | Pistacia miochinensis |
| 2 | Platycarya miocenica |
| 1, 2 | **Pterocarya serrulata** |
| 2 | Podogonium knorrii |
| 1, 2 | Polygonum miosinicum |
| 2 | Populus balsamoides |
| 2 | Populus glandulifera |
| 2 | Populus latior |
| 2 | Populus simonii |
| 2 | Potamogeton sp. |
| 2 | Prunus miobrachypoda |
| 2 | Pueraria miothunbergiana |
| 1, 2 | Q. miovariabilis |
| 1, 2 | Q. sinomiocenicum |
| 1, 2 | Quercus dissimilifolia |
| 1 | Reveesia sp. |
| 1 | **Rhododendron sp.** |
| 2 | Rhus miosuccedania |
| 2 | Rosa shanwangensis |
| 1 | **Rosaceae gen. et spec. indet.** |
| 1, 2 | **Salix angusta** |
| 1, 2 | **Salix masamunei** |
| 1, 2 | **Salix miosinica** |
| 2 | Sapindus shandongensis |
| 2 | Shaniodendron subequale |
| 2 | Sophora miojaponica |
| 2 | Spiraea mioblumei |
| 2 | Stachyurus parachinensis |
| 2 | Tapiscia pseudochinensis |
| 2 | Tetrastigma shantungensis |
| 1 | Thymelaeaceae gen. et spec. indet. |
| 1, 2 | **Tilia miochinensis** |
| 1, 2 | **Tilia miohenryana** |
| 1, 2 | **Tilia preamurensis** |
| 2 | Toona bienensis |
| 2 | **U. cf. multinervis** |
| 1, 2 | **Ulmus macrocarpa** |
| 1, 2 | **Ulmus miopumila** |

| | **Shanwang flora, China** (continued) |
|---|---|
| 1, 2 | **Ulmus paralaciniata** |
| 2 | Wisteria fallax |
| 2 | Vitis romanetii |
| 2 | Zanthoxylum prunifolium |
| 1, 2 | Zelkova ungeri |
| 2 | Zizyphus miojujuba |

Boldface indicates that the genus is present in the Selárdalur-Botn Formation. Grey shading indicates that the genus is present in the younger Brjánslækur-Seljá and Tröllatunga-Gautshamar formations (12 and 10 Ma). *1* based on pollen, spores, *2* based on leaves and/or fruit/seed fossils,3 based on leaf fossils

## Appendix 4.2

Floristic composition of the 15 Ma sedimentary formation of Iceland compared to contemporaneous northern hemispheric fossil assemblages at higher latitudes and to one older assemblage from eastern North America (Floral lists from Matthews and Ovenden 1990; Whitlock and Dawson 1990; Tiffney 1994; Traverse 1994; Fyles et al. 1994; White and Ager 1994; Graham 1999; Liu and Basinger 2000).

| | **Brandon Lignite, Vermont [43°50′N]** Early Miocene Tiffney 1994 [3]; Traverse 1994 [1]; Graham 1999 [1, 3] |
|---|---|
| 1, 3 | Alangium |
| 3 | Caldesia |
| 3 | Caricoidea (Cyperaceae) [extinct genus] |
| 1, 3 | Carya |
| | Castanea |
| 1 | **Cathaya** |
| | Clethra ? |
| 3 | Cleyera (Eurya) |
| | Corylus ? |
| 3 | Cyrilla |
| | Engelhardia |
| 3 | **Ericaceae** |
| 3 | Euodia |
| | **Fagus** |
| | fern spores (unidentified) |
| | **Glyptostrobus** |
| 1, 3 | Gordonia |
| | Gramineae |
| | Horniella (Rutaceae) [extinct genus] |
| 1, 3 | **Ilex (2 spp.)** |
| 3 | Illicium |
| | Juglans |
| | Jussiaea |
| | Liquidambar |
| | Lyonia (?) |
| 3 | **Magnolia (2 spp.)** |
| | Manilkara (Sapotaceae) |
| 3 | Melliodendron |
| 3 | Microdiptera (Lythraceae) [extinct genus] |
| | Mimusops (Sapotaceae) |
| 3 | Moroidea [extinct genus] |
| | Morus |
| | Nestronia (?) (Santalaceae) |
| 1, 3 | Nyssa (4 spp.) |
| | Oxydendrum (?) |
| 3 | **Parthenocissus** |
| 3 | Persea |
| 3 | Phellodendron |
| | Pinus (haploxylon type) |
| | **Pinus (sylvestris type)** |
| | Planera |
| | **Pterocarya** |
| 1, 3 | Quercus |
| | Rhamnus |
| | **Rhododendron** |
| | Rhus |
| | **Rosaceae (?)** |
| 1, 3 | Rubus |
| 3 | Sargentodoxa |
| | Siltaria (Fagaceae) [extinct genus] |
| 1, 3 | Symplocos (2 spp) |
| | **Tilia** |
| | Toddalieae (Rutaceae) |
| 3 | Turpinia |
| | **Ulmus** |
| | Vaccinium |
| 1, 3 | Vitis (2 spp.) |
| 3 | Zanthoxylum (3) |
| 3 | Zenobia (Ericaceae) |

(continued)

**Porcupine River, Central Alaska [67°20′N]**
Middle Miocene, 15 Ma White and Ager 1994

| | |
|---|---|
| 1 | Anaemia-type |
| 1 | Deltoidospora sp. |
| 1 | fungal spores |
| 1 | Laevigatosporites sp. |
| 1 | Lycopodium annotinum/complanatum |
| 1 | Osmunda sp. |
| 1 | **Polypodiaceae/Dennstaedtiaceae** |
| 1 | Sphagnum |
| | Abies sp. |
| 1 | **Picea sp. (large)** |
| 1 | **Picea spp.** |
| 1 | Pinaceae undiff. (bisaccates) |
| 1 | **Pinus (robust corpus)** |
| 1 | **Pinus koraiensis-type** |
| 1 | **Pinus spp.** |
| 1 | Sciadopitys |
| 1 | **Taxodiaceae (papillate)** |
| 1 | **Taxodiaceae-Cupressaceae-Taxaceae** |
| 1 | **Tsuga canadensis-type** |
| 1 | **Tsuga heterophylla-type** |
| 1 | **Tsuga mertensiana** |
| 1 | **Tsuga sp.** |
| 1 | **? Acer sp. A** |
| 1 | **? Acer sp. B** |
| 1 | ? Cornus sp. |
| 1 | **Alnus sp. (4-pored)** |
| 1 | **Alnus sp. (5-pored)** |
| 1 | Alnus sp. (6-pored) |
| 1 | Alnus sp. (7-pored) |
| 1 | **Betula sp. (<20 μm)** |
| 1 | **Betula sp. (>20 μm)** |
| 1 | Carya sp. |
| 1 | Castanea-type |
| 1 | **Cercidiphyllum sp.** |
| 1 | **cf. Carpinus sp.** |
| 1 | cf. Corylus sp. |
| 1 | cf. Galium sp. |
| 1 | cf. Juncus sp. |
| 1 | **Ericales** |
| 1 | **Fagus sp.** |
| 1 | **Ilex-type** |
| 1 | **Iridaceae/Liliaceae** |
| 1 | Juglans sp. |
| 1 | Larix/Pseudotsuga |
| 1 | Liquidambar sp. |
| 1 | Ludwigia sp. |
| 1 | Nymphaea sp. |
| 1 | Nyssa sp. |
| 1 | **Pterocarya sp.** |
| 1 | Quercus sp. |
| 1 | Rhus-type |
| 1 | **Salix sp.** |
| 1 | **Tilia-type** |
| 1 | **Ulmus-type** |

**Ballast Brook Formation, Banks Island [74°20′N]**
Middle Miocene
Fyles et al. 1994

| | |
|---|---|
| 2 | Azolla sp. |
| 2 | Salvinia sp. (?) |
| 2 | **Glyptostrobus sp.** |
| 2 | **Juniperus sp.** |
| 2 | Metasequoia sp. |
| 2 | Thuja sp. |
| 2 | Abies sp. |
| 2 | Larix sp. |
| 2 | **Picea sp.** |
| 2 | **Pinus 3-needle type** |
| 2 | **Pinus contorta-banksiana type** |
| 2 | **Pinus densiflora-resinosa type** |
| 2 | **Pinus itelmenorum** |
| 2 | **Pinus paleodensiflora** |
| 2 | **Pinus sp.** |
| 2 | **Pinus subsect. Eustrobi** |
| 2 | Pseudotsuga sp. |
| 2 | **Tsuga sp.** |
| 2 | Coniferales undet. |
| 2 | Aldrovanda sp. |
| 2 | **Alnus (Alnobetula) sp.** |
| 2 | **Alnus incana type** |
| 2 | **Alnus sp.** |
| 2 | Andromeda polifolia |
| 2 | Aracispermum sp. (?) |
| 2 | Aracites |
| 2 | Aracites globosa |
| 2 | Aralia sp. |
| 2 | **Betula apoda type** |
| 2 | Carex spp. |
| 2 | cf. Paliurus |
| 2 | Cladium sp. |
| 2 | Comptonia sp. |
| 2 | Cornus canadensis type |
| 2 | Cornus stolonifera type (?) |

(continued)

| **Ballast Brook Formation, Banks Island** (continued) | |
|---|---|
| 2 | Damasonium type |
| 2 | Decodon gibbosus type |
| 2 | Decodon globosus type |
| 2 | Diervilla sp. |
| 2 | Dulichium sp. |
| 2 | Epigaea sp. |
| 2 | Epipremnum crassum |
| 2 | Epipremnum ornatum |
| 2 | Hamamelidaceae? |
| 2 | Hippuris sp. |
| 2 | Hypericum sp. |
| 2 | **Juglandaceae Genus?** |
| 2 | Liriodendron sp. |
| 2 | Menyanthes (< 2mm) |
| 2 | Menyanthes trifoliata |
| 2 | Microdiptera/Mneme type |
| 2 | Mitella sp. |
| 2 | Morus sp. |
| 2 | Myrica eogale type |
| 2 | Myrica sp. |
| 2 | Najas sp. (?) |
| 2 | Nigrella sp. |
| 2 | Nymphoides sp. |
| 2 | Phyllanthus sp. |
| 2 | Polanisia cf. sibirica |
| 2 | Potamogeton sp. |
| 2 | Potentilla sp. |
| 2 | Ranunculus lapponicus |
| 2 | Rubus sp. |
| 2 | Rynchospora sp. |
| 2 | **Salix sp.** |
| 2 | Sambucus sp. |
| 2 | Saururus sp. |
| 2 | Scirpus sp. |
| 2 | Sparganium sp. |
| 2 | Teucrium sp. |
| 2 | Tubela type |
| 2 | Weigelia sp. |
| 2 | Zenobia sp. |

| **West River, Horton River, N.W.T. [69°12′N]** | |
|---|---|
| Early Miocene | |
| Whitlock and Dawson 1990 | |
| 2 | Chara/Nitella type |
| 2 | Metsequoia sp. |
| 2 | Abies sp. |
| 2 | Larix sp. |
| 2 | **Picea sp.** |
| 2 | Pinus five-needle type undiff. |
| 2 | **Tsuga sp.** |
| 2 | Actinidia sp. |
| 2 | Aracites globosa |
| 2 | Aralia sp. |
| 2 | **Betula sp.** |
| 2 | Carex sp. |
| 2 | Carex spp. |
| 2 | Decodon sp. |
| 2 | Hippuris sp. |
| 2 | Lycopus sp. |
| 2 | Menyanthes trifoliata |
| 2 | Nuphar sp. |
| 2 | Paliurus sp. |
| 2 | Potamogeton sp. |
| 2 | Rubus sp. |
| 2 | Rumex sp. |
| 2 | Sambucus sp. |
| 2 | Solanum/Physalis type |
| 2 | Sparganium sp. |
| 2 | Weigela sp. |
| 2 | Viola sp. |
| 2 | Vitis sp. |

| **Mary Sachs Gravels, Banks Island [75°57′N]** | |
|---|---|
| Early Miocene | |
| Matthews and Ovenden 1990 | |
| 2 | **Glyptostrobus sp.** |
| 2 | Metasequoia sp. |
| 2 | Metasequoia disticha |
| 2 | Taxodium sp. |
| 2 | Thuja occidentalis |
| 2 | Abies grandis |
| 2 | Larix omoloica |
| 2 | Larix sp. |
| 2 | **Picea banksii** |
| 2 | **Picea sp.** |
| 2 | Pinus five-needle type undiff. |
| 2 | Pinus funebris |
| 2 | Pinus itelmenorum |
| 2 | Pinus paleodensiflora |
| 2 | Actinidia sp. |
| 2 | **Alnus (Alnobetula) sp.** |
| 2 | **Alnus incana** |
| 2 | Andromeda polifolia |
| 2 | Aralia sp. |
| 2 | Arctostaphylos alpina/rubra type |

(continued)

| | **Mary Sachs Gravels, Banks Island** (continued) |
|---|---|
| 2 | **Betula apoda** |
| 2 | **Betula arboreal type** |
| 2 | **Betula dwarf shrub type** |
| 2 | Carex sp. |
| 2 | Chamaedaphne sp. |
| 2 | Chenopodium sp. |
| 2 | Cleome sp. |
| 2 | Comptonia spp. |
| 2 | Diervilla sp. |
| 2 | Dulichium vespiforme |
| 2 | Epipremnum crassum |
| 2 | Hypericum sp. |
| 2 | Juglans eocineria |
| 2 | Liriodendron sp. |
| 2 | Ludwigia sp. |
| 2 | Menyanthes small form |
| 2 | Microdiptera/Mneme type |
| 2 | Morus sp. |
| 2 | Myrica (Gale) sp. |
| 2 | Myrica eogale |
| 2 | Paliurus sp. |
| 2 | Phyllanthus sp. |
| 2 | Polanisia sp. |
| 2 | Potamogeton sp. |
| 2 | Potentilla sp. |
| 2 | Ranunculus (Batrachium) sp. |
| 2 | Ranunculus hyperboreus |
| 2 | Rubus sp. |
| 2 | Rumex sp. |
| 2 | Sagisma sp. |
| 2 | Sambucus sp. |
| 2 | Sedum sp. |
| 2 | Sesuvium sp. |
| 2 | Solanum/Physalis type |
| 2 | Sparganium sp. |
| 2 | Teucrium sp. |
| 2 | Weigela sp. |
| 2 | Verbena sp. |

| | **Haughton Formation, Devon Island [75°22′N]** Early Miocene Whitlock and Dawson 1990 [1] |
|---|---|
| 1 | Abies |
| 1 | **Acer** |
| 1 | **Alnus** |
| 1 | **Betula** |
| 1 | Brassicaceae |
| 1 | Carya |
| 1 | [Castanea] |
| 1 | **cf. Fagus** |
| 1 | cf. Fraxinus |
| 1 | Chenopodiaceae |
| 1 | Corylus type |
| 1 | **Cupressaceae** |
| 1 | Cyperaceae |
| 1 | Dryopteris type |
| 1 | **Ericales** |
| 1 | [Gleichenidites] |
| 1 | **[Ilex]** |
| 1 | Juglans |
| 1 | Larix |
| 1 | [Liquidambar] |
| 1 | Lycopodium type |
| 1 | Osmunda type |
| 1 | **Ostrya/Carpinus** |
| 1 | **Picea** |
| 1 | **Pinus** |
| 1 | Pinus strobus type |
| 1 | [Platanus][a] |
| 1 | Populus |
| 1 | Potamogeton |
| 1 | Pteridium type |
| 1 | **Pterocarya** |
| 1 | Quercus |
| 1 | **Salix** |
| 1 | Sparganium |
| 1 | Sphagnum type |
| 1 | **Tsuga** |
| 1 | **Ulmus/Zelkov** |

[a]Mentioned in text but not shown in pollen diagram

Boldface indicates that the genus is present in the Selárdalur-Botn Formation. Grey shading indicates that the genus is present in the younger Brjánslækur-Seljá and Tröllatunga-Gautshamar formations (12 and 10 Ma). *H* herbaceous plant, *W* water plant. *1* based on pollen, spores; *2* based on leaves and/or fruit/seed fossils; *3* based on leaf fossils

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## Explanation of Plates

**Plate 4.1** **1**–**4**. Selárdalur valley, Northwest Iceland, Selárdalur-Botn Formation (ca 15 Ma). **1**. Selárdalur valley, view towards NE. **2**. Mount Þórishlíðarfjall, base camp at valley floor, outcrop on slopes in centre. **3**. Outcrop showing volcanic plant-bearing sediments. **4**. Fossils preserved as impressions in volcanic rock. **5**–**8**. Botn in Súgandafjörður, Northwest Iceland, Selárdalur-Botn Formation (15 Ma). **5**. Botn Farm next to outcrop. **6**. Outcrop showing organic-rich clastic sediments. **7**. Alternation of organic-rich coal seams, siltstones, and ash layers. **8**. Fossils preserved as compressions with intact organic material in clastic sediments

**Plate 4.2** **1**–**3**. *Polypodium* sp. 1. **1**. Spore in LM, polar view showing monolete tetrad mark. **2**. Spore in SEM, proximal polar view. **3**. Detail of spore surface. **4**–**6**. Polypodiaceae gen. et spec. indet. 1. **4**. Spore in LM, equatorial view. **5**. Spore in SEM, equatorial view. **6**. Detail of spore surface

**Plate 4.3** **1–3**. Cupressaceae gen. et spec. indet. 1 (*Cryptomeria* sp). **1**. Pollen grain in SEM. **2**. Detail of pollen grain surface. **3** Pollen grain in LM. **4–6**. Cupressaceae gen. et spec. indet. 3 (*Juniperus* sp.) **4**. Pollen grain in SEM. **5**. Detail of pollen grain surface showing tectum with few orbiculae. **6**. Pollen grain in LM. **7–9**. Cupressaceae gen. et spec. indet. 3 (*Juniperus* sp.) **7**. Pollen grain in SEM. **8**. Detail of pollen grain surface. **9**. Pollen in LM. **10–13**. Cupressaceae gen. et spec. indet. 3 (*Juniperus* sp.) **10**. Pollen in SEM. **11**. Detail of pollen grain surface showing tectum with orbiculae. **12**. Detail of pollen grain surface showing verrucate to regulate tectum elements with a microechinate suprasculpture around ulcus. **13**. Pollen grain in LM

**Plate 4.4** **1–3**. Cupressaceae gen. et spec. indet. 2 (*Glyptostrobus* sp.) **1**. Pollen grain in SEM. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM. **4–6**. Cupressaceae gen. et spec. indet. 2 (*Glyptostrobus* sp.) **4**. Pollen grain in SEM. **5**. Pollen grain surface with orbiculae. **6**. Ruptured pollen grain in LM. **7–11**. *Glyptostrobus europaeus* (Brongn.) Unger. **7**. Seed cone (IMNH 4988). **8**. Long-shoot (IMNH 4975). **9**. Short-shoot (IMNH 4999). **10**. Axes with scale leaves (IMNH 5002-01). **11**. Epidermal cuticle with stomata (IMNH 5002-01). **12**. *Glyptostrobus pensilis* (Staunton ex D. Don) K. Koch for comparison. Epidermal cuticle with stomata

**Plate 4.5** **1–4**. Cupressaceae gen. et spec. indet. 4 (*Sequoia* sp.) **1**. Pollen grain in SEM showing leptoma with papilla. **2**. Detail of papilla with orbiculae. **3**. Pollen grain in LM. **4**. Detail of pollen grain surface showing leptoma area. **5**. to **8**. *Sequoia abietina* (Brongn.) Knobl. **5**. Leafy axis (IMNH 4998). **6**. Detail showing alternate phyllotaxis (IMNH 4987). **7**. Epidermal cuticle with stomata (IMNH 4979). **8**. Epidermal cuticle without stomata (IMNH 4978)

**Plate 4.6** **1–3**. *Cathaya* sp. **1**. Bisaccate pollen grain in SEM, polar view. **2**. Detail of saccus. **3**. Pollen grain in LM, polar view. **4–7**. *Pinus* sp. 1 (Diploxylon type). **4**. Bisaccate pollen grain in SEM, polar view. **5**. Detail of corpus and saccus. **6**.. Detail of corpus. **7**. Pollen grain in LM. **8–10**. *T*suga sp. 1. 8. Monosaccate pollen grain in SEM. 9. Detail of monosaccus and corpus, distal polar view. 10. Pollen grain in LM, polar view

**Plate 4.7** **1–3**. *Ilex* sp. 1. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface in mesocolpium and aperture region. **3**. Pollen grain in LM, equatorial view. **4–6**. *Ilex* sp. 1. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface showing clavae with short striate suprasculpture in mesocolpium and aperture region. **6**. Pollen grain in LM, equatorial view. **7–9**. *Alnus* sp. 1. **7**. Tetraporate pollen grain in SEM, polar view. **8**. Detail of pollen grain surface. **9**. Pollen in LM, polar view. **10–12**. *Alnus* sp. 1. **10**. Pentaporate pollen grain in SEM, polar view. 11. Detail of pollen grain surface. 12. Pollen grain in LM, polar view

**Plate 4.8** **1–3**. *Alnus* sp. 1. **1**. Pollen grain in SEM, polar view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM. **4–6**. *Betula* sp. 1. **4**. Pollen grain in SEM, polar view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, polar view. **7–9**. *Betula* sp. 1. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, oblique polar view. **10–12**. *Carpinus* sp. 1. **10**. Pollen grain in SEM, polar view. 11. Detail of pollen grain surface. 12. Pollen grain in LM, polar view

**Plate 4.9** **1–3**. *Viburnum* sp. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4–6**. *Viburnum* sp. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7–9**. *Viburnum* sp. **7**. Pollen grain in SEM, equatorial view. 8. Detail of pollen grain surface. 9. Pollen grain in LM, equatorial view

**Plate 4.10** **1–3**. *Ceridiphyllum* sp. **1**. Pollen grain in SEM, polar view. **2**. Detail of pollen grain surface showing aperture membrane. **3**. Detail of pollen grain surface showing microreticulum with irregularly distributed microechinae. **4**. Pollen grain in LM, polar view. **5–6**. *Cercidiphyllum* sp. **5**. Leaf fragment (IMNH 6686-A01). **6**. Detail showing crenate leaf margin (IMNH 6686-B01)

**Plate 4.11** **1–3**. *Rhododendron* sp. 1 (*R. ponticum* type). **1**. Pollen tetrad in SEM. **2**. Detail of tetrad surface showing microrugulate tectum. **3**. Tetrad in LM. **4–7**. *Rhododendron* sp. 1. **4**. Pollen tetrad with viscin threads in SEM. **5**. Detail of tetrad surface. **6**. Tetrad in LM. **7**. Detail of pollen grain surface showing tectum with viscin thread. **8**. *Rhododendron* sp. 1. Detail of showing microrugulate tectum. **9**. cf.. *Rhododendron* sp. (IMNH 289-04)

**Plate 4.12** **1–12**. *Fagus friedrichii* Grímsson and Denk. **1–6**. Pollen. **1**. Pollen grain in SEM, equatorial view. **2**. Pollen grain in SEM, polar view. **3**. Pollen grain in LM, equatorial view. **4**. Pollen grain in LM, equatorial view. **5**. and **6**. Details of surface showing regulate tectum. **7–9**. Cupules. **7**. Pedunculate cupule showing position of two nutlets (IMNH 5001-02). **8**. Cupule valve showing spine-like appendages (IMNH 4997). **9**. Cupule valve showing recurved apical appendages (IMNH 5002-04). **10–12**. Leaves. **10**. Large wide elliptic leaf (IMNH 299). **11**. Narrow elliptic leaf (IMNH 16). **12**. Wide elliptic leaf (IMNH 782). **13**. Bud scale (IMNH 5061)

**Plate 4.13** **1–3**. *Pterocarya* sp. **1**. Pollen grain in SEM, polar view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, polar view. **4–6**. *Pterocarya* sp. **4**. Pollen grain in SEM, polar view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, polar view. **7–9**. Liliaceae gen. et spec. indet. 1. **7**. Pollen grain in SEM, distal polar view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM. **10–12**. Liliaceae gen. et spec. indet . 1. **10**. Pollen grain in SEM, proximal polar view showing sulcus. **11**. Detail of pollen grain surface. **12**. Pollen in LM

**Plate 4.14** **1, 2, 5** and **6**. *Platanus* sp. **1**. Tricolpate pollen grain in SEM, equatorial view. **2**. Pollen grain in LM, equatorial view. **5**. Detail of aperture membrane. **6**. Detail of tectum. **3, 4, 7** and **8**. *Platanus* sp. **3**. Pollen grain in SEM, equatorial view. **4**. Pollen grain in LM, equatorial view. **7**. Detail of pollen grain surface showing closed reticulum. **8**. Detail of pollen grain surface. **9**. *Platanus leucophylla* (Unger) Knobloch, weakly lobed leaf (IMNH 302)

**Plate 4.15** **1–3**. *Sanguisorba* sp. 1. **1**. Pollen grain in SEM, polar view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, polar view. **4–6**. Rosaceae gen. et spec. indet. 1. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface showing aperture region. **6**. Pollen grain in LM, equatorial view. **7–9**. Rosaceae gen. et spec. indet. 2. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface showing aperture region. **9**. Pollen grain in LM, equatorial view. **10–12**. Rosaceae gen. et spec. indet. 3. **10**. Pollen grain in SEM, equatorial view. **11**. Detail of pollen grain surface showing aperture region. **12**. Pollen grain in LM, equatorial view

**Plate 4.16** **1–3**. *Salix* sp. 1. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface showing wide reticulum and aperture rim. **3**. Pollen grain in LM, equatorial view. **4–6**. *Salix* sp. 1. **4**. Pollen group in SEM. **5**. Pollen group in LM. **6**. Pollen group at higher magnification. **7–9**. *Salix* sp. 1. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface close to aperture rim. **9**. Pollen grain in LM

**Plate 4.17** **1–3**. *Acer* sp. 1. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface showing striate tectum. **3**. Pollen grain in LM, equatorial view. **4–6**. *Acer* sp. 2. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface showing striate-rugulate tectum. **6**. Pollen grain in LM, equatorial view. **7–9**. *Aesculus* sp. **7**. Large leaflet (IMNH 783). **8**. Lower part of leaflet (IMNH 748). **9**. Detail of 8. showing leaflet margin

**Plate 4.18** **1**–**4**. *Tilia* sp. **1**. Pollen grain in SEM, polar view. **2**. Detail of aperture region showing tectum and aperture membrane. **3**. Detail of pollen surface showing microreticulate tectum. **4**. Pollen grain in LM, polar view. **5**. and **6**. *Tilia selardalense* Grímsson, Denk and Símonarson. **5**. Leaf fragment with petiole and deeply cordate base (IMNH 5555). **6**. Complete weakly lobed leaf (s.n.)

**Plate 4.19** **1, 3** and **5**. *Ulmus* sp. **1**. Pollen grain in SEM, polar view. **3**. Pollen grain in LM, polar view. **5**. Detail of pollen grain surface around porus. **2, 4** and **6**. *Ulmus* sp. **2**. Pollen grain in SEM, polar view. **4**. Pollen grain in LM, polar view. **6**. Detail of pollen grain surface showing slightly annulate porus. **7**–**9**. *Ulmus* sp. MT1 **7**. Leaf with serrate leaf margin (IMNH 304). **8**. Detail of leaf margin (IMNH 305). **9**. Leaf margin (IMNH 6684-03)

**Plate 4.20** **1**–**3**. *Tetracentron atlanticum*. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface showing striatoreticulate tectum and aperture. **3**. Pollen grain in LM, equatorial view. **4**–**6**. *Parthenocissus* sp. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface showing microreticulate to reticulate tectum in polar region. **6**. Pollen grain in LM, equatorial view. **7**–**9**. Pollen type 1. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface showing regulate/fossulate tectum. **9**. Pollen grain in LM, equatorial view. **10**–**12**. Pollen type 1. **10**. Pollen grain in SEM, equatorial view showing smooth aperture rim. **11**. Detail of fossulate tectum. **12**. Pollen grain in LM, equatorial view

## Plates




**Plate 4.1**

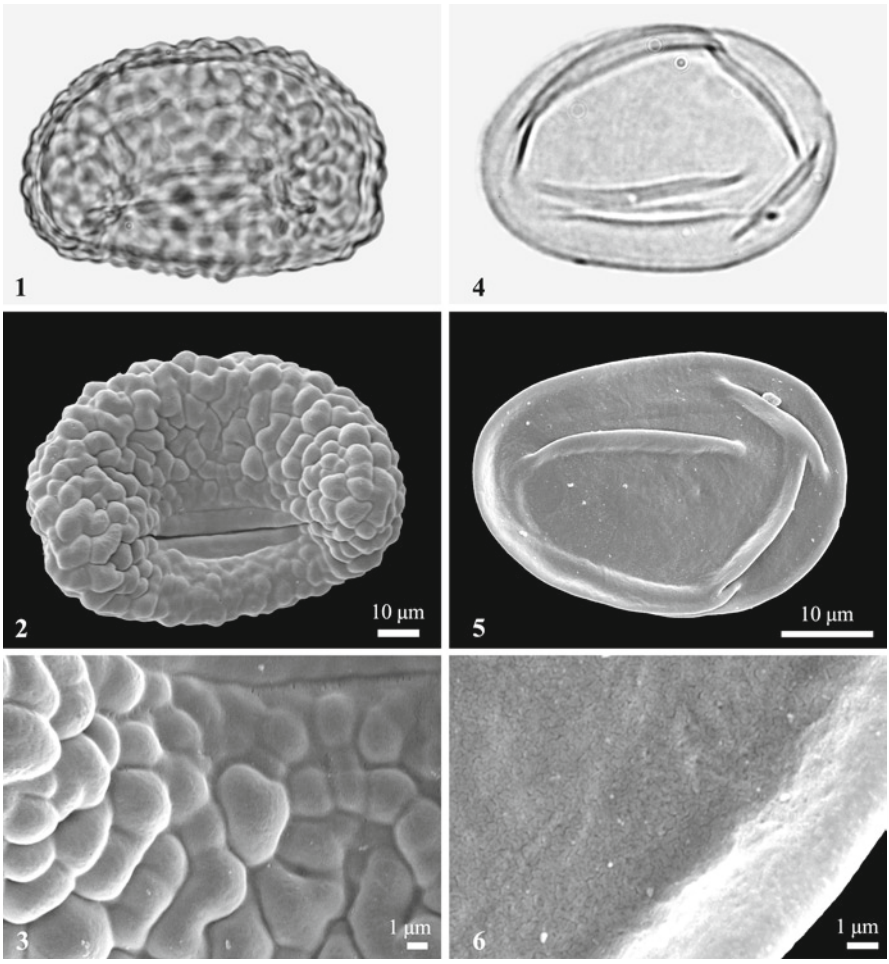



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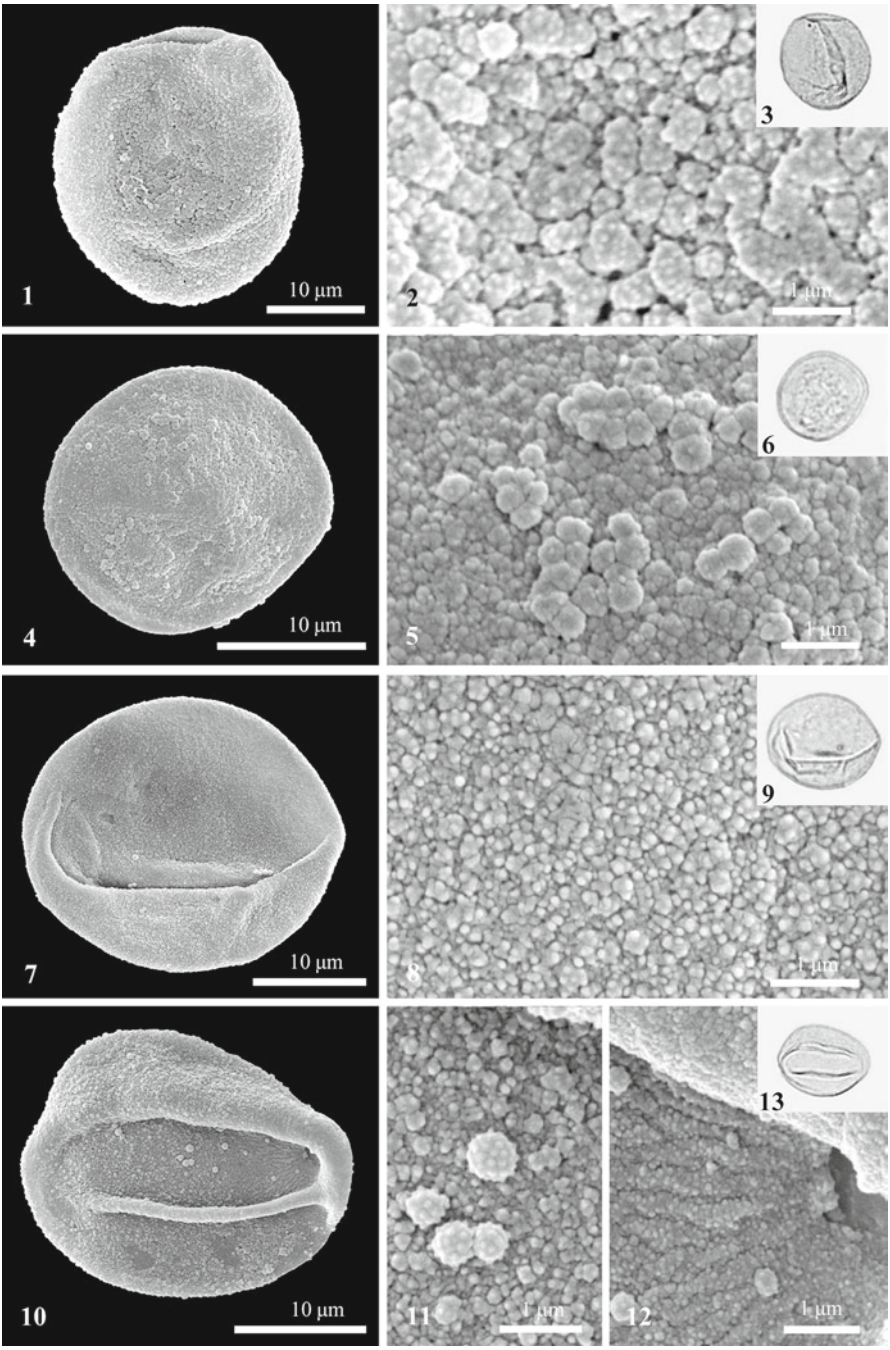



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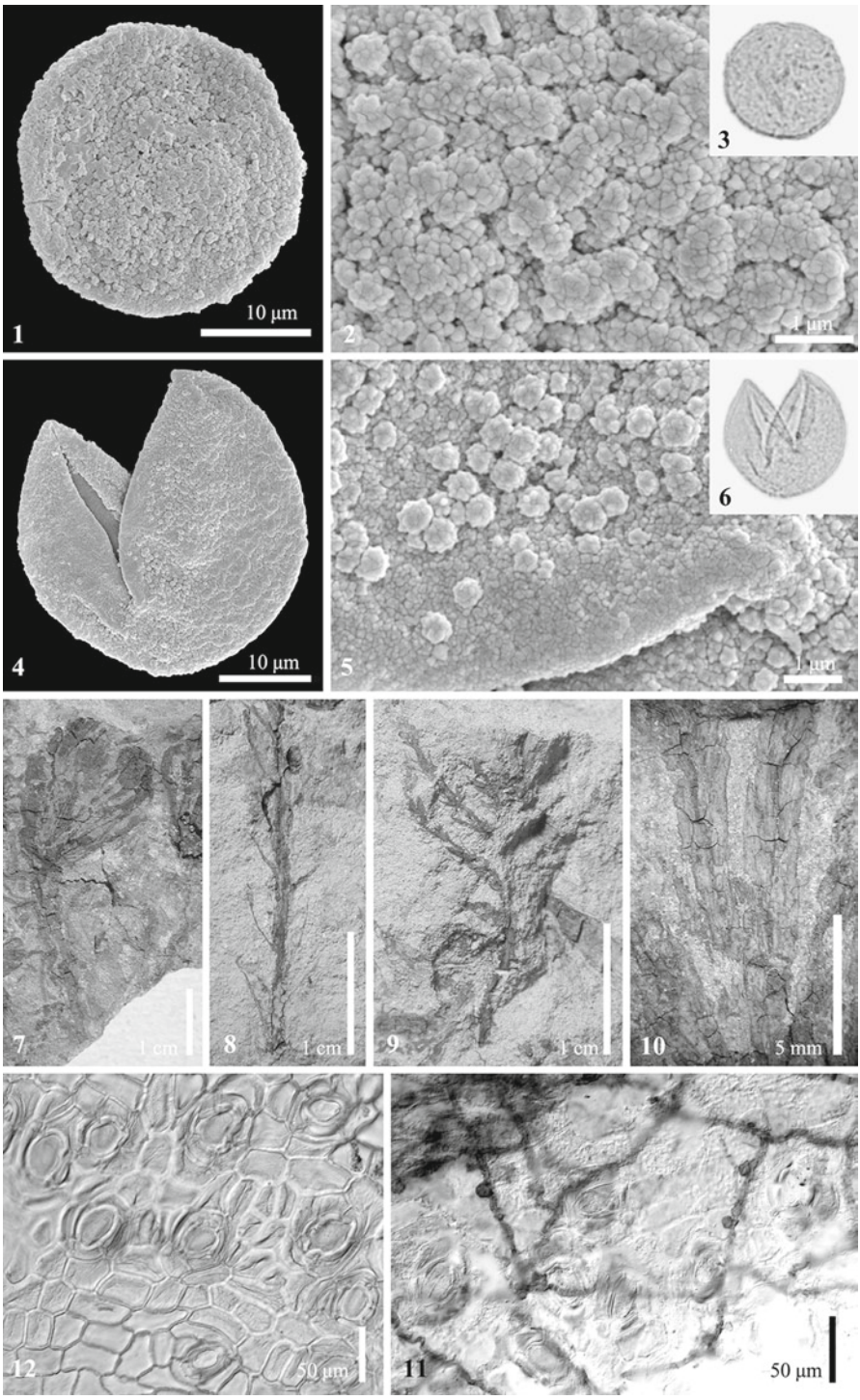



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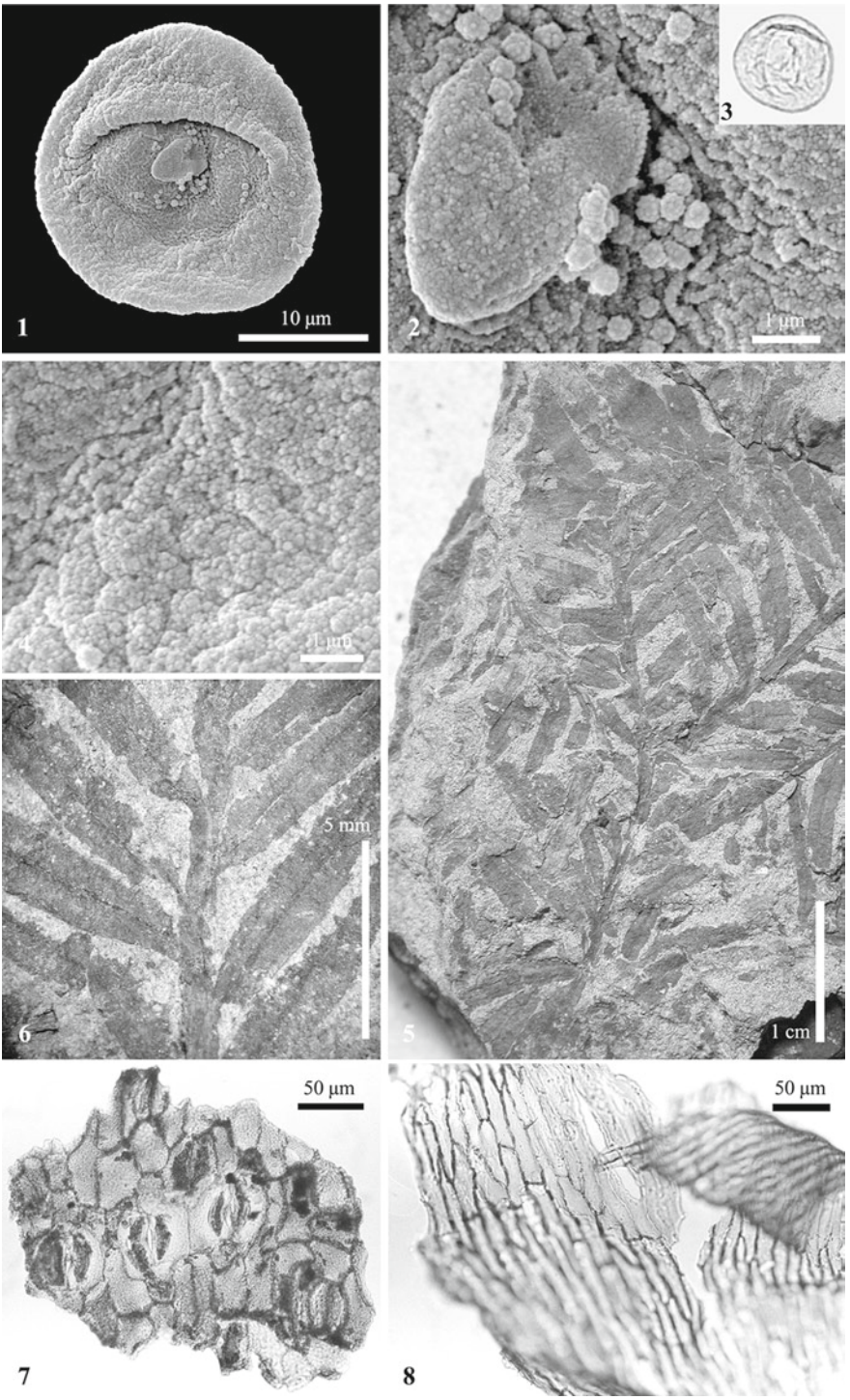



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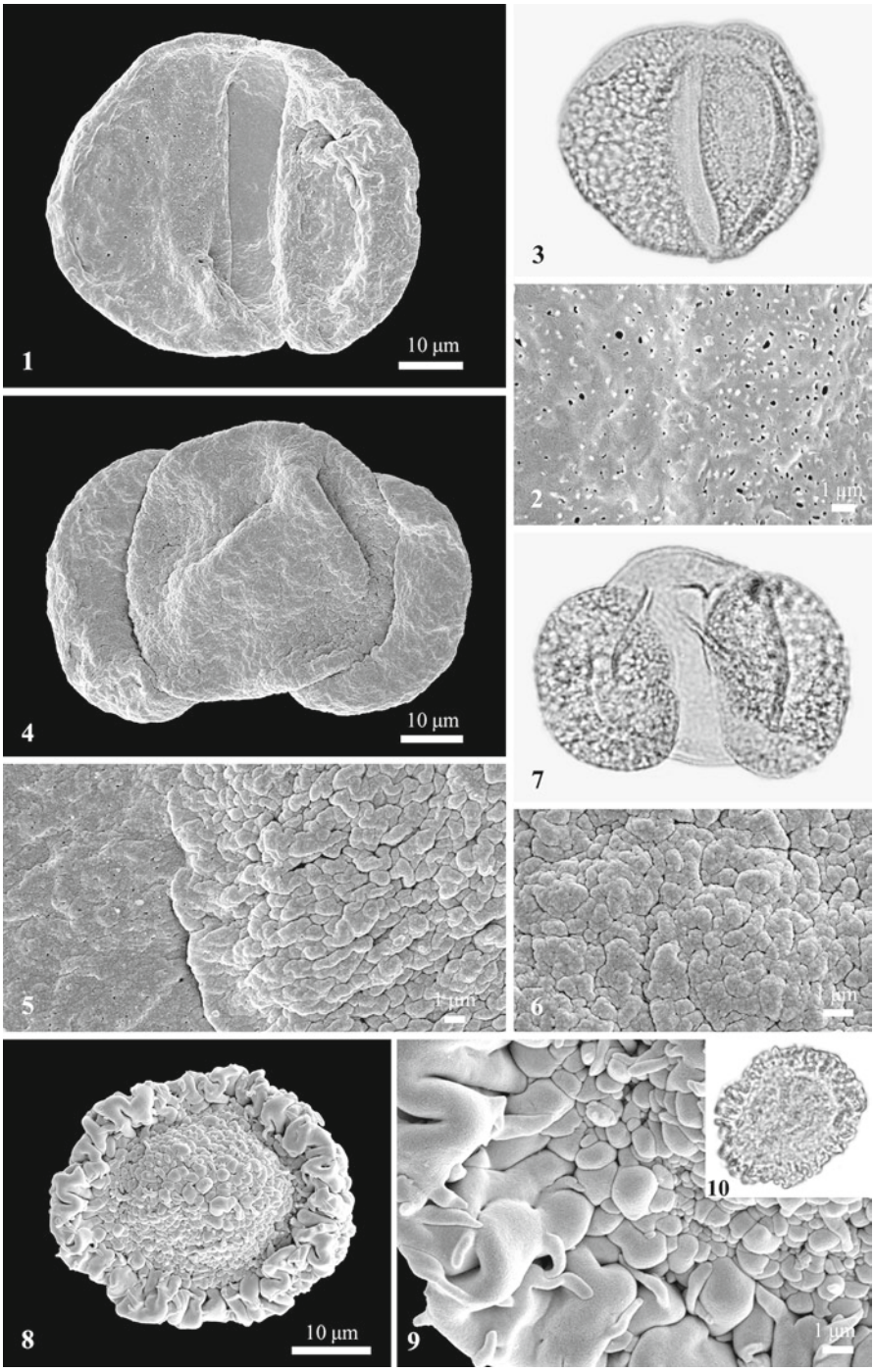



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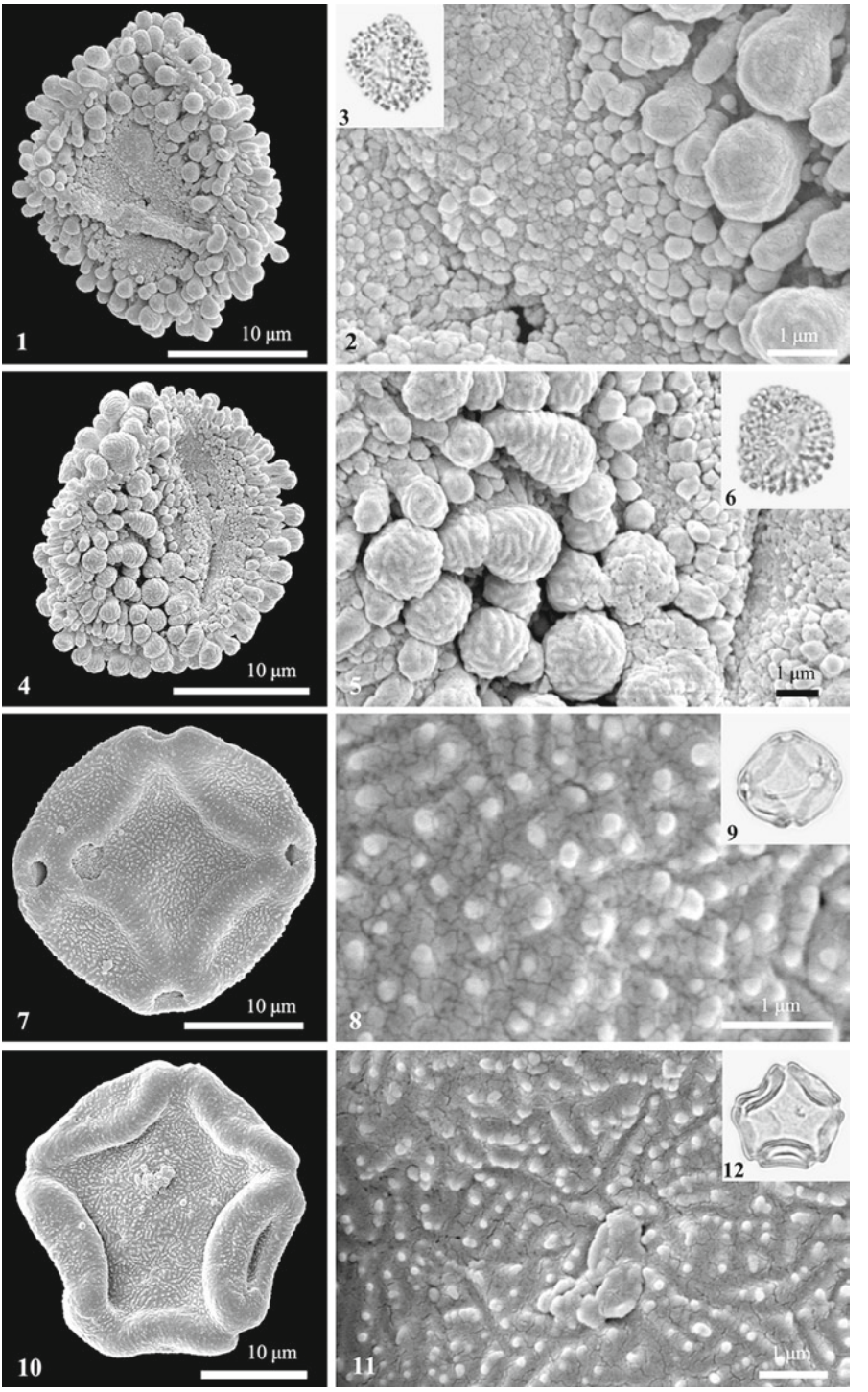



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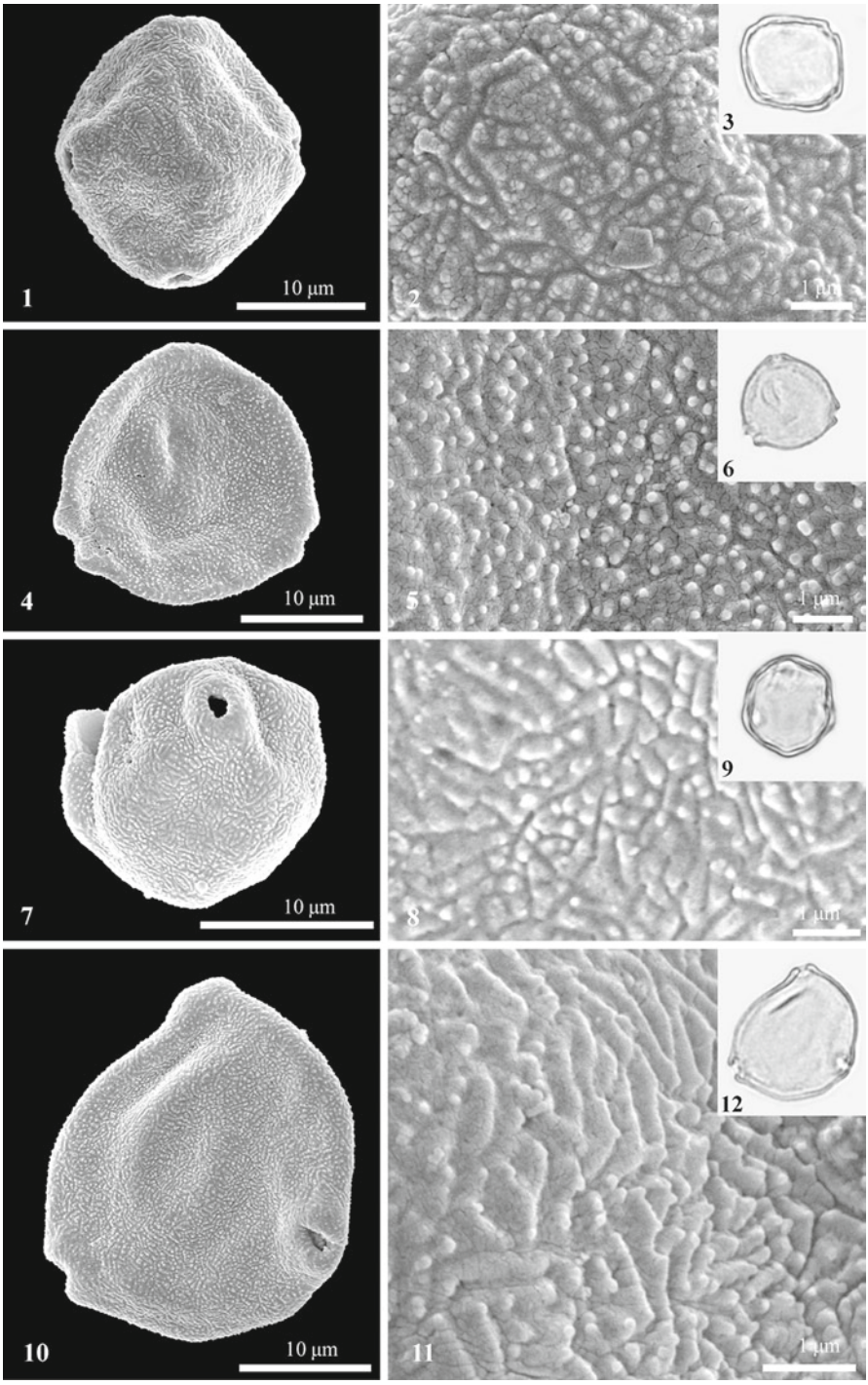



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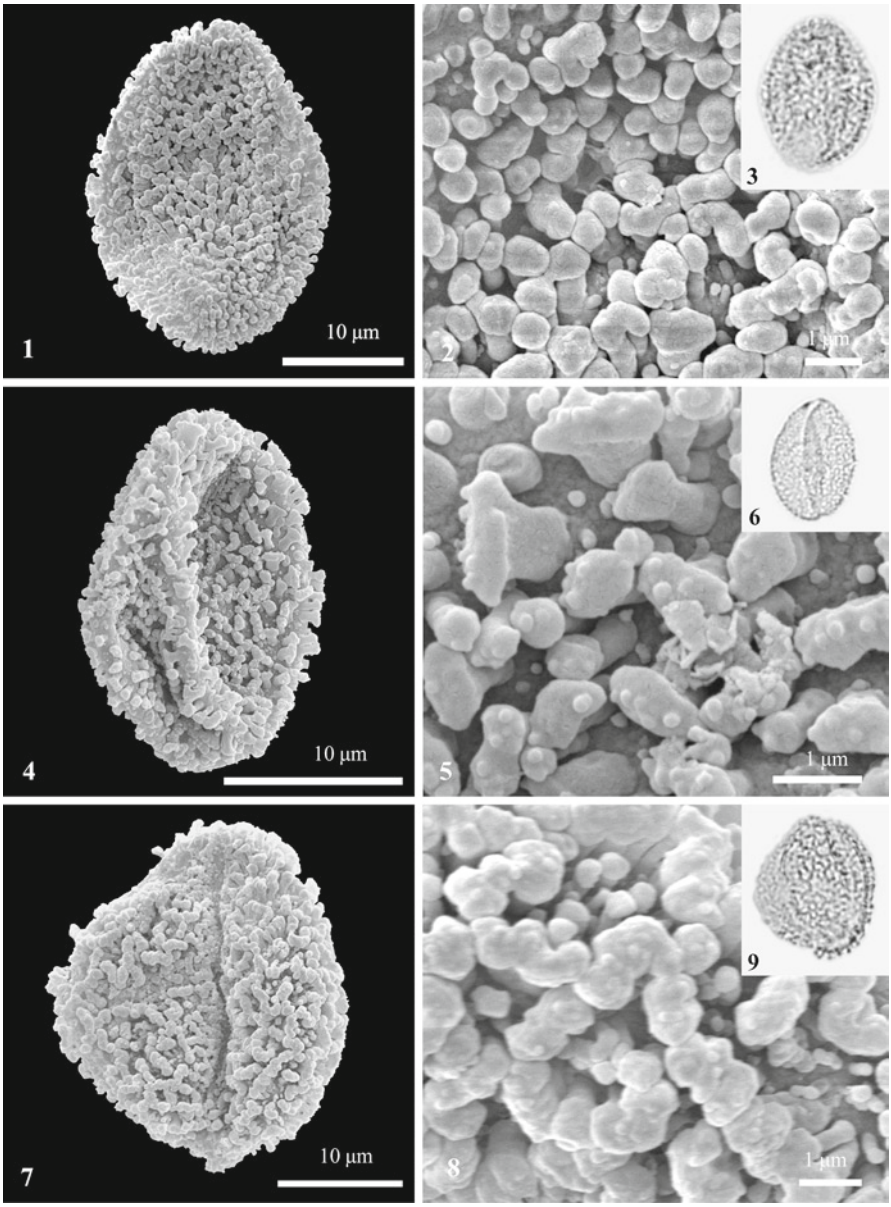



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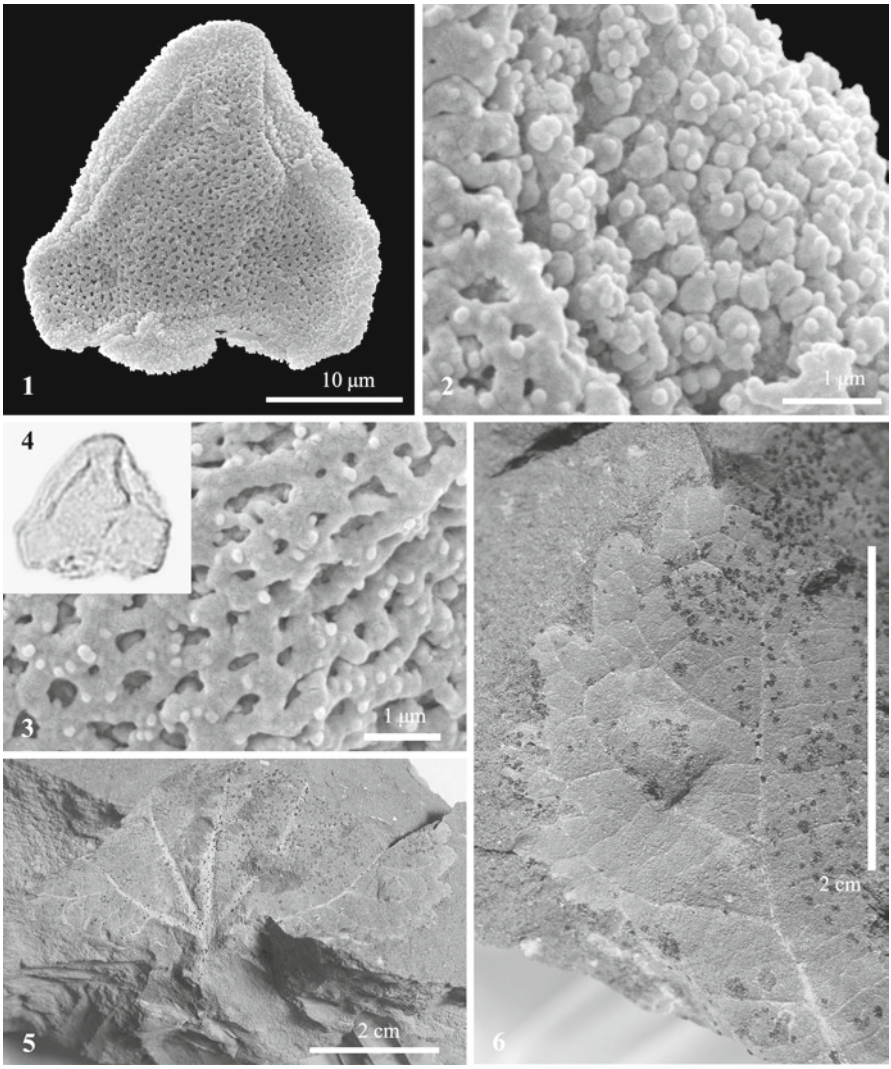



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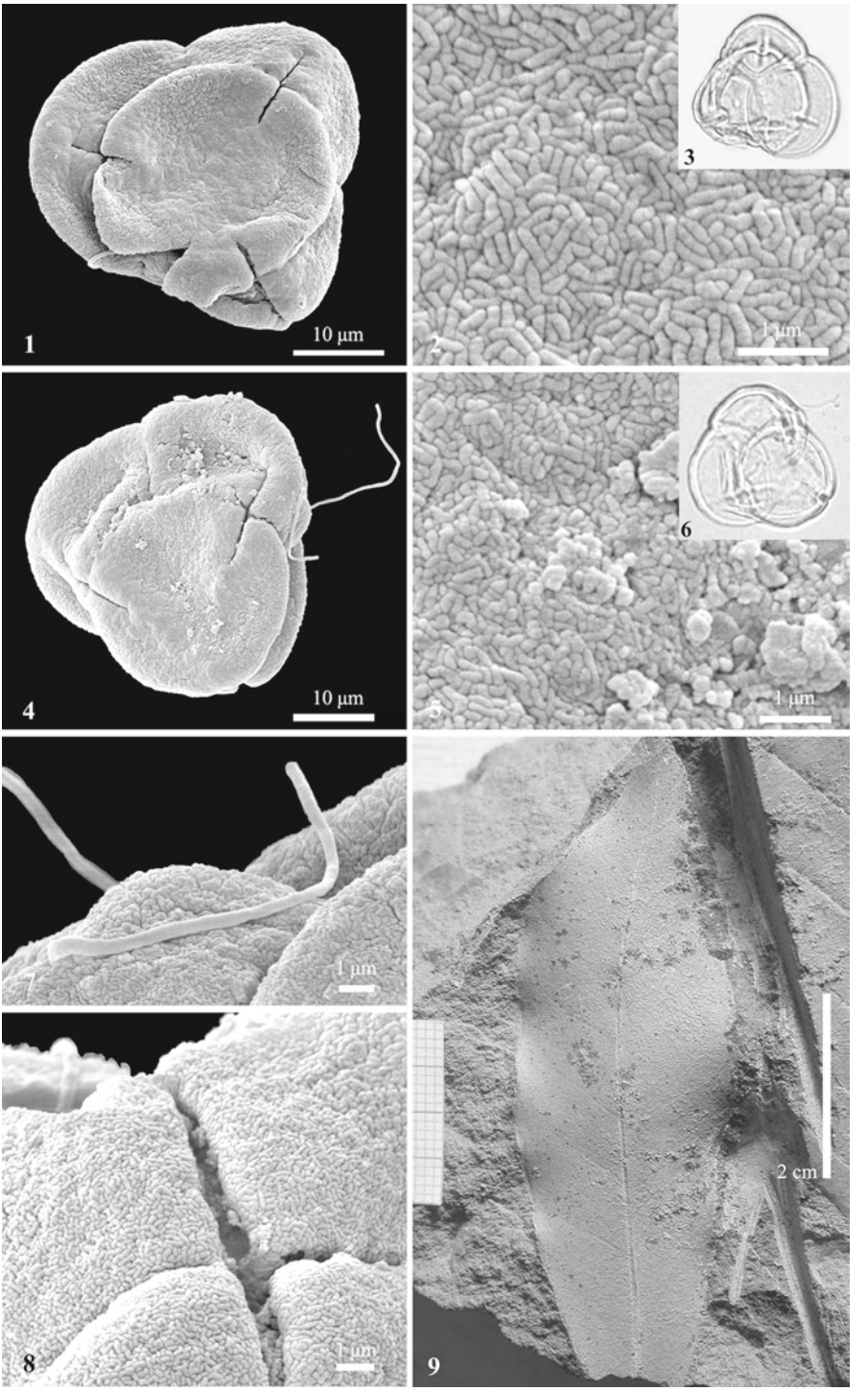



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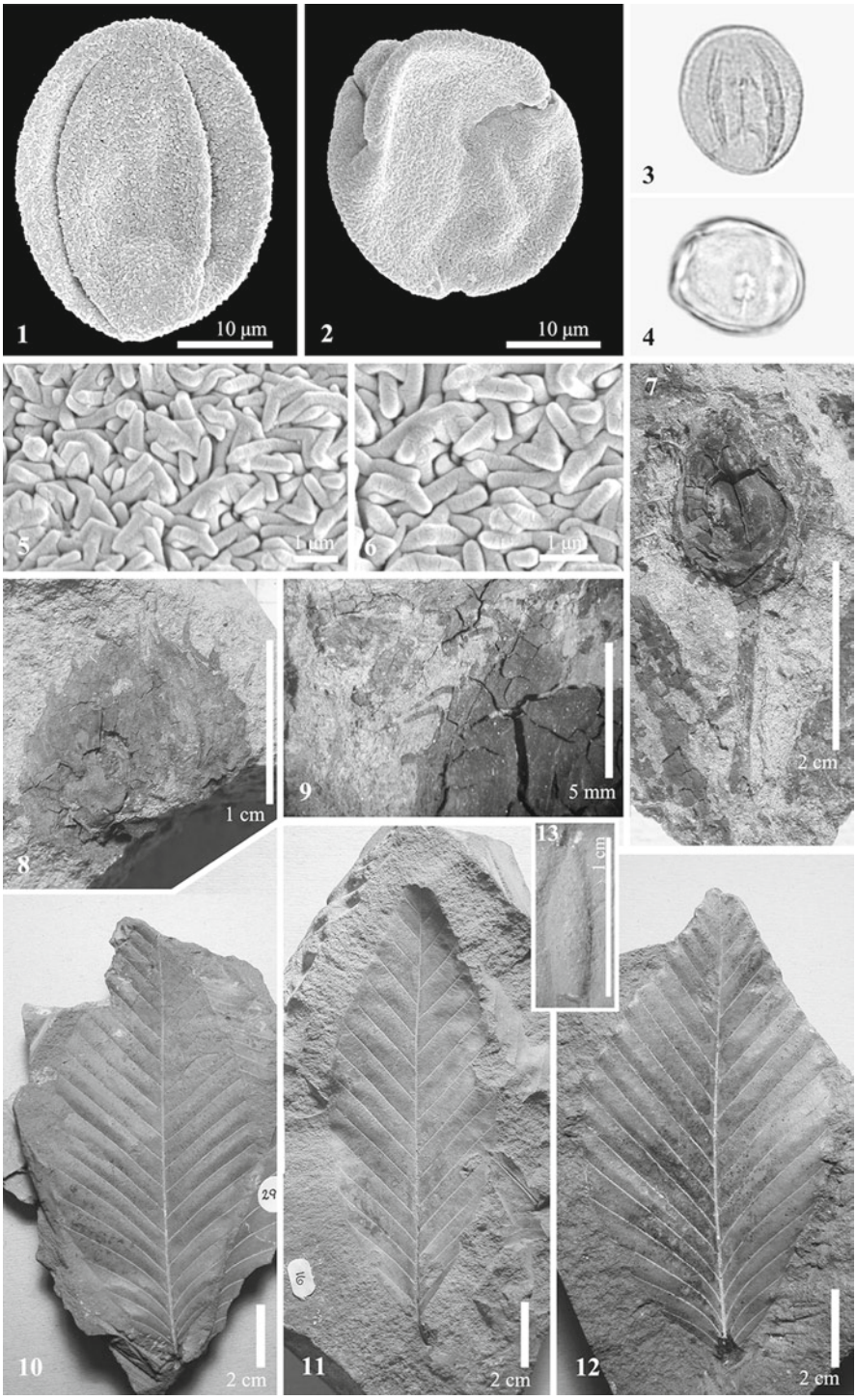

1
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4
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1 µm
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**Plate 4.12**

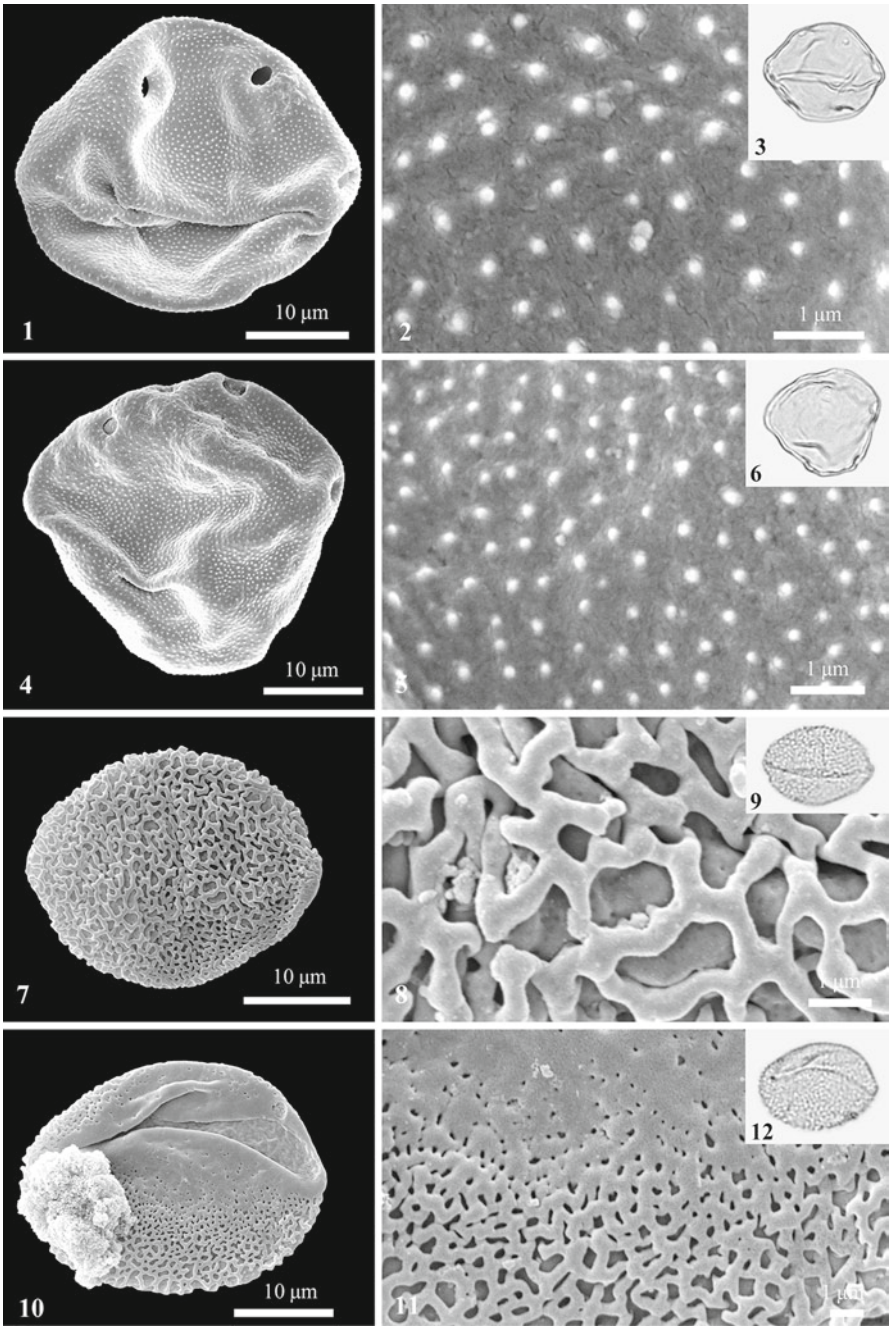



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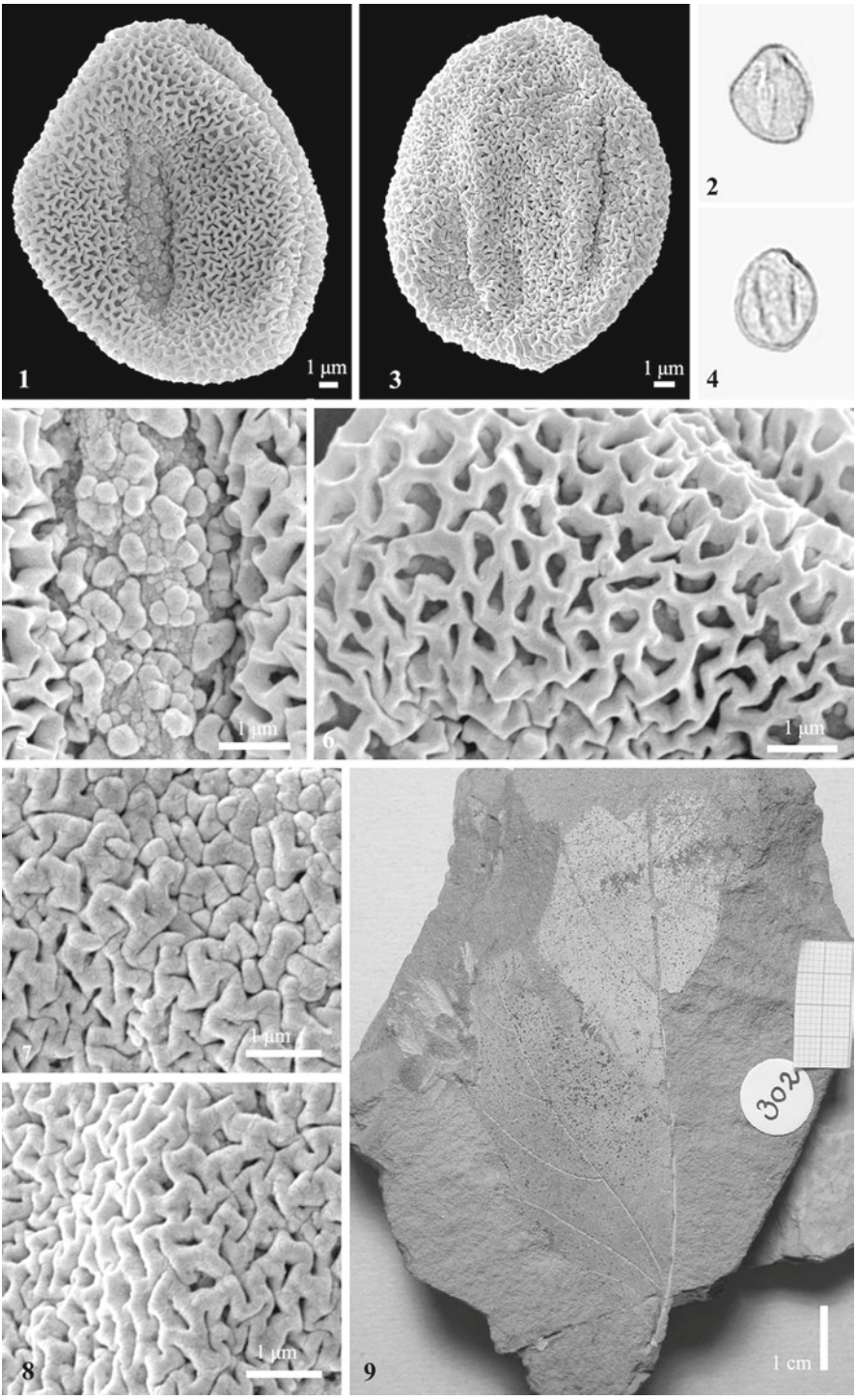



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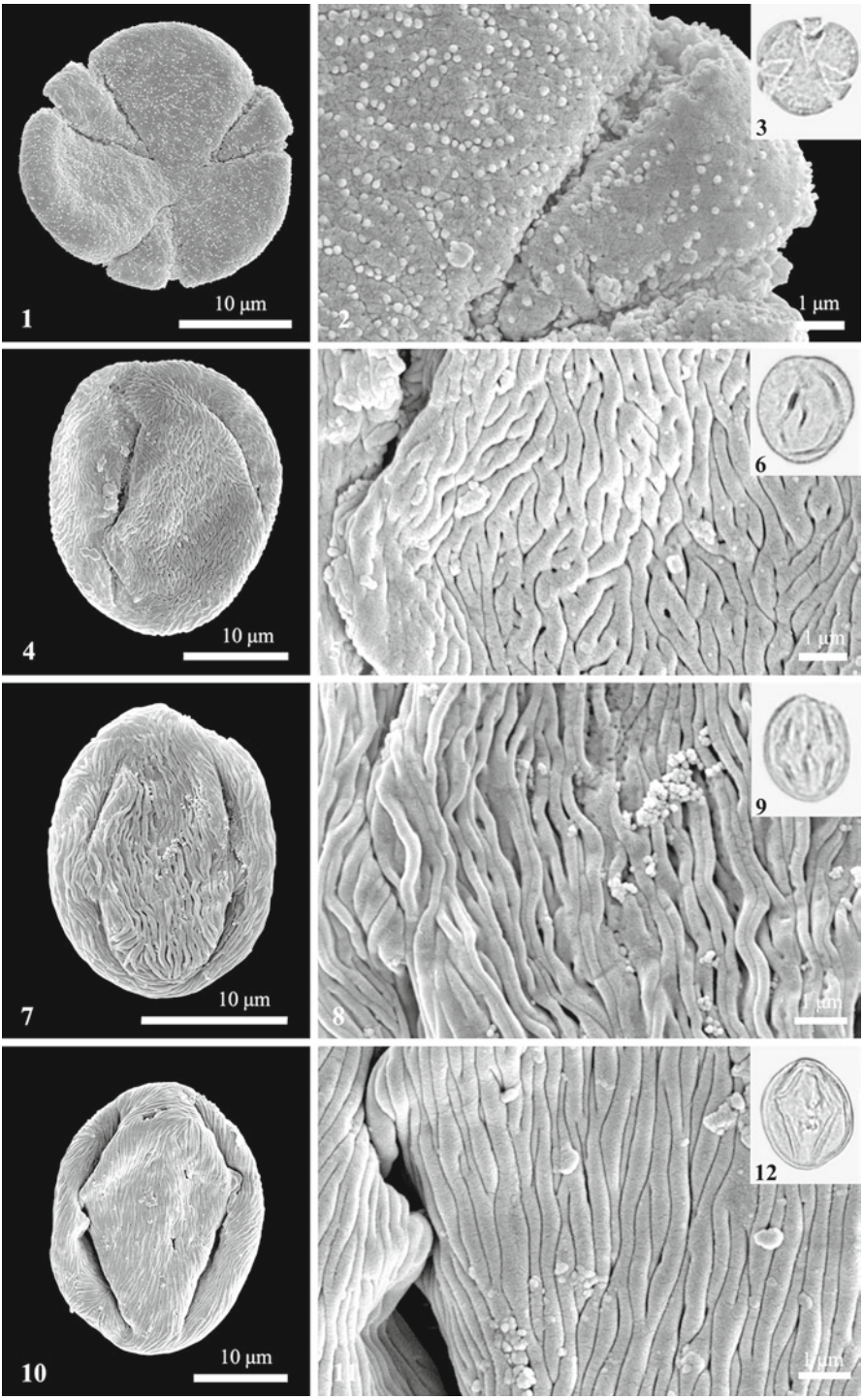



**Plate 4.15**

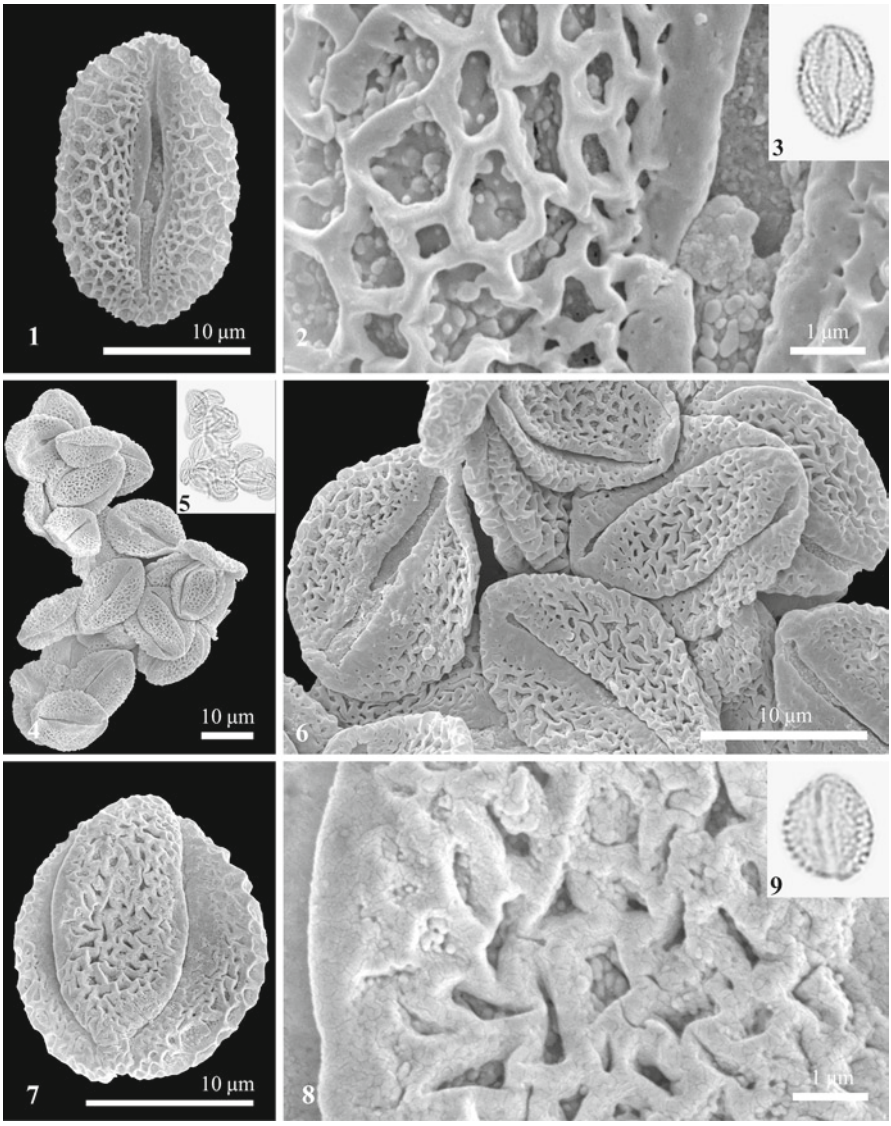



**Plate 4.16**

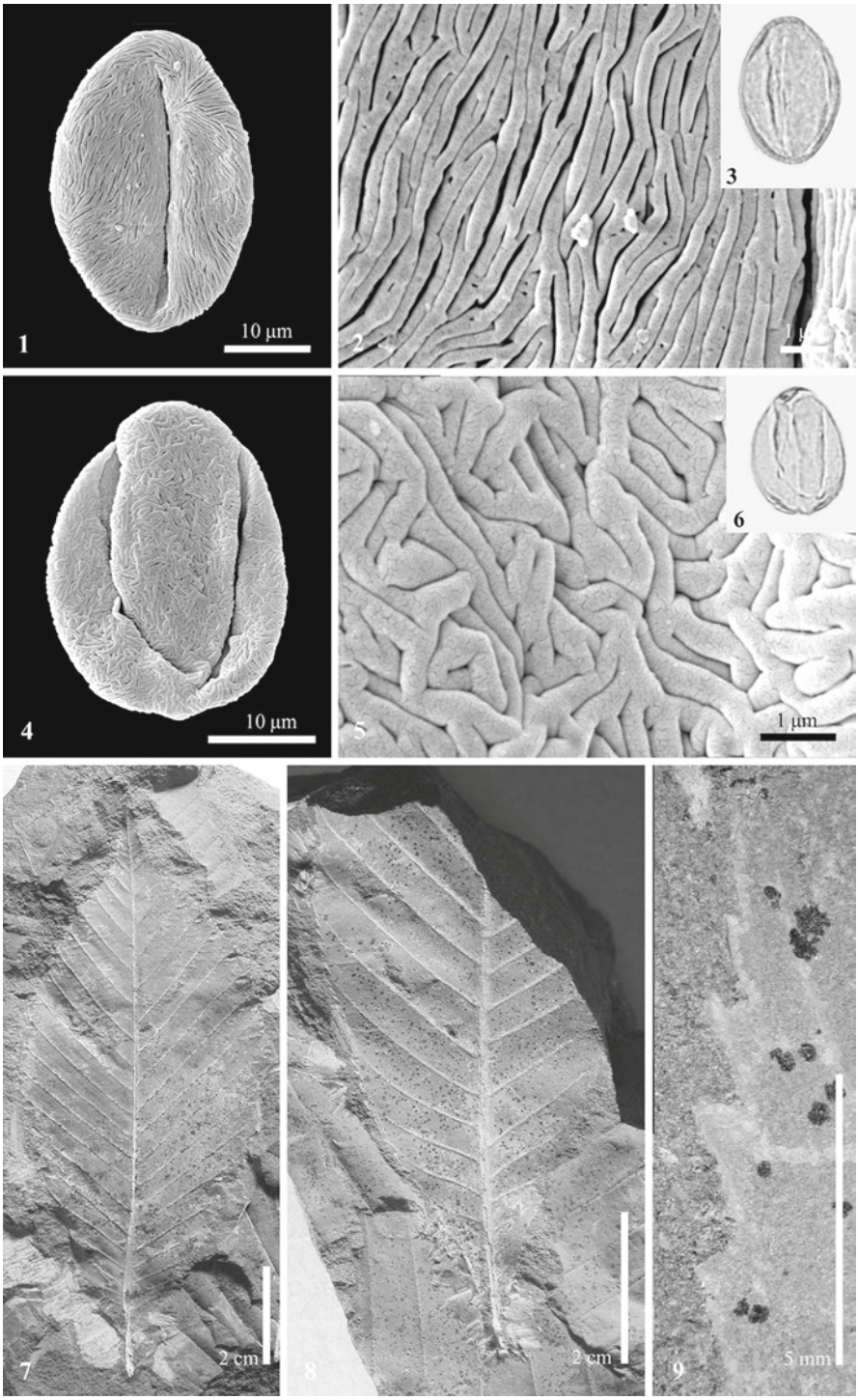



**Plate 4.17**

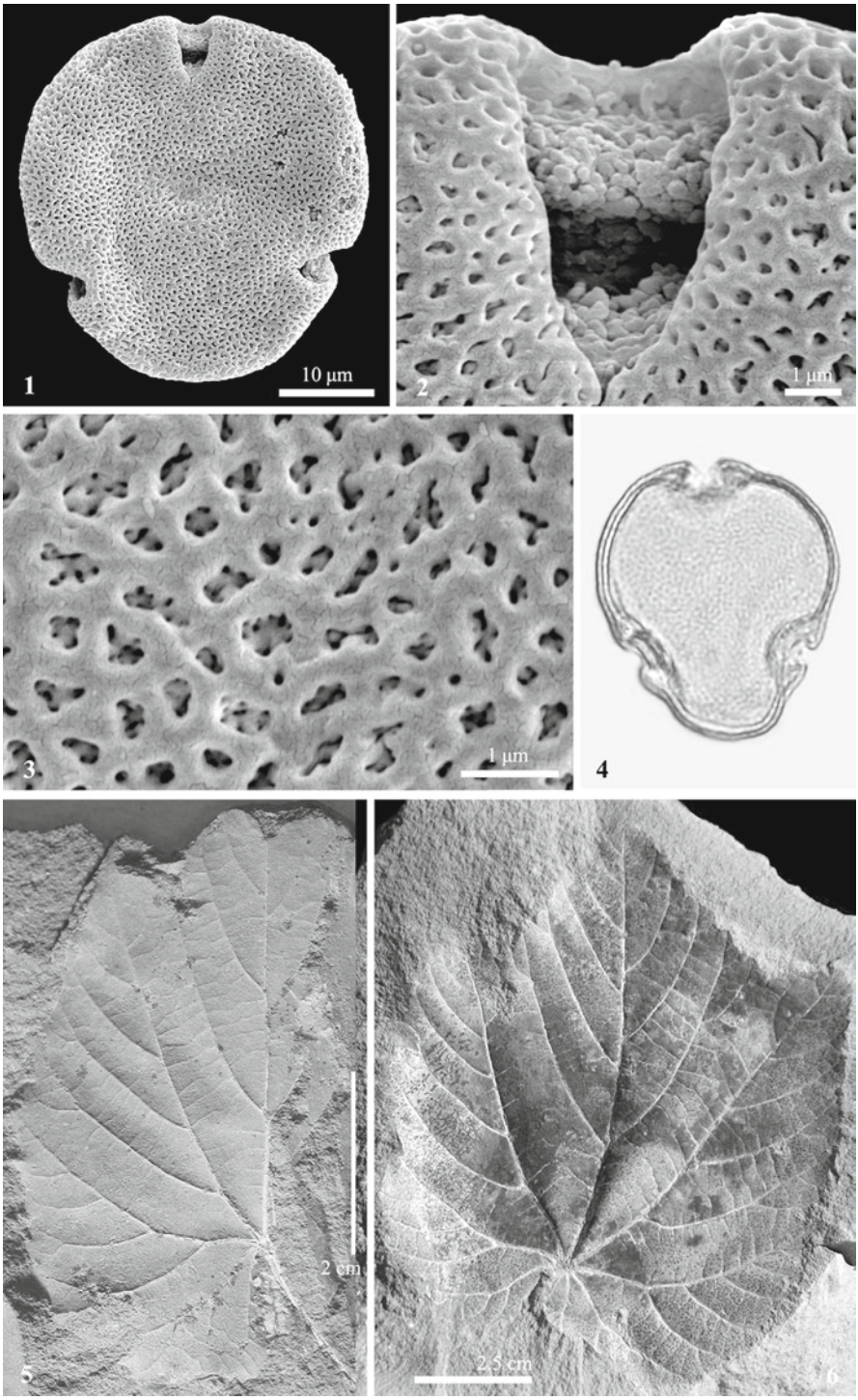



**Plate 4.18**

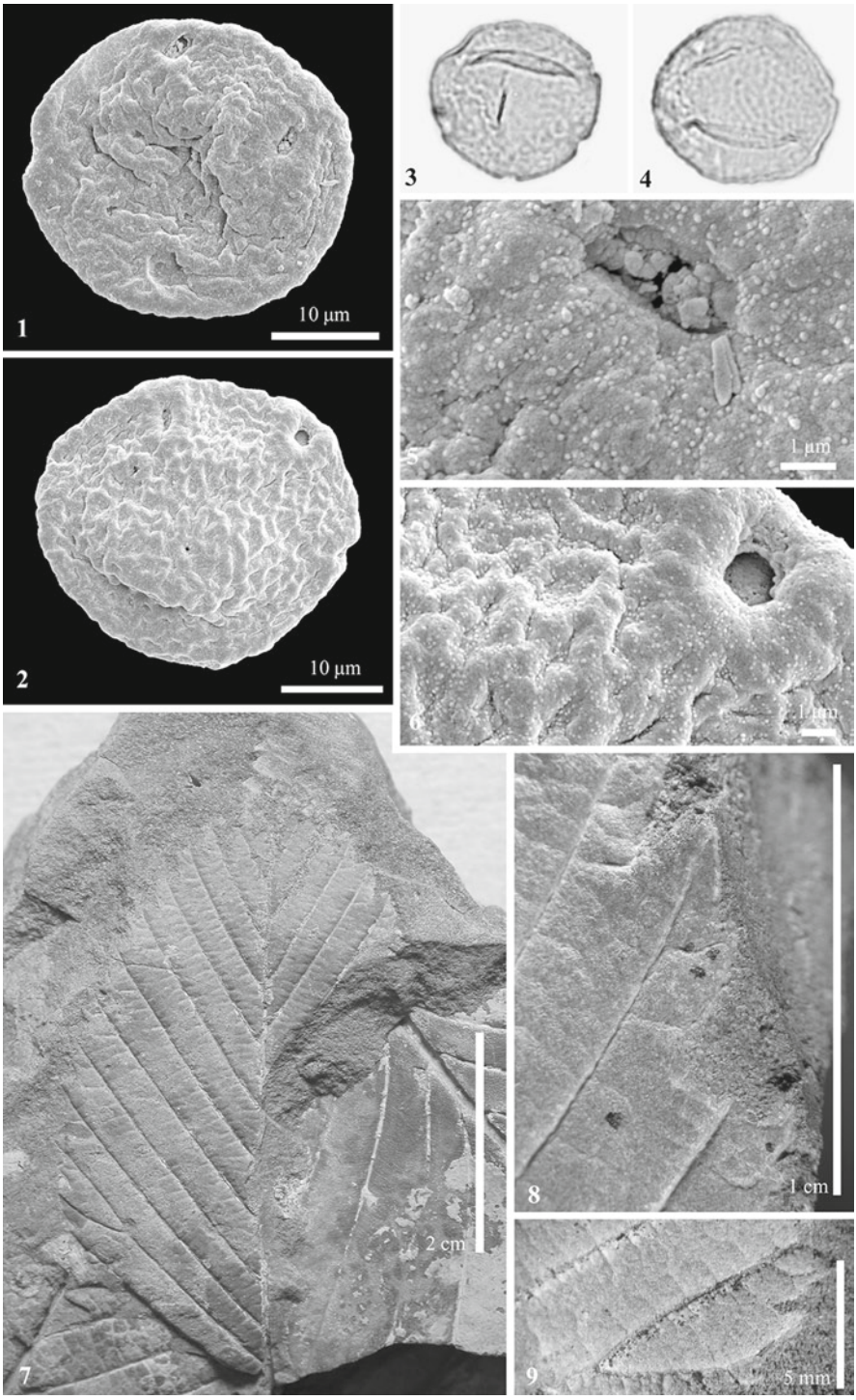



**Plate 4.19**

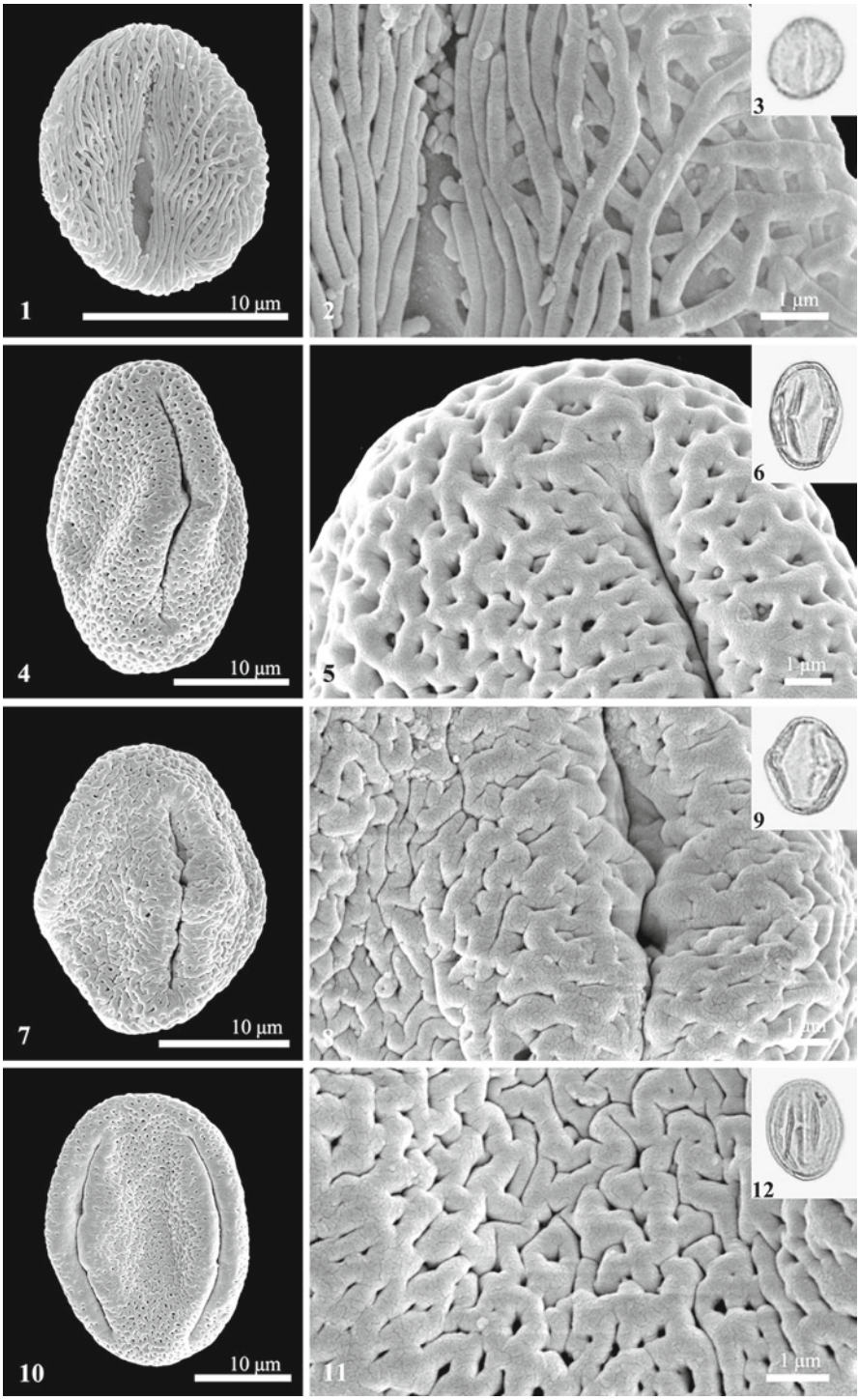



**Plate 4.20**

# Chapter 5
# The Classic Surtarbrandur Floras

**Abstract** The classic Surtarbrandur floras of Iceland are 12 Ma (late Serravallian) and belong to the Brjánslækur-Seljá Formation. They make up the most diverse macroflora known from the Miocene of Iceland, with the highest number of exotic angiosperms recorded from this period (*Laurophyllum*, *Liriodendron*, *Magnolia*, *Platanus*, and *Sassafras*). Unlike in the older and younger floras, *Fagus* is absent from the macrofossil and pollen record, suggesting that the older *F. friedrichii* had not yet been replaced by the later immigrating *F. gussonii*. The plant assemblages recovered from the Brjánslækur-Seljá Formation represent azonal riparian lowland and upland forests and zonal hardwood forests in the vicinity of a lake followed higher up by mixed broad-leaved deciduous and conifer forests. The plant assemblages reflect the culmination of warm and moist vegetation in Iceland in the late Serravallian. The climatic and vegetation optimum recorded in Iceland for this stage does not reflect the general trend of cooling after the Mid-Miocene Climatic Optimum (17–15 Ma), as seen in many other floras in the northern hemisphere.

## 5.1 Introduction

Plant fossils from Surtarbrandsgil had already been mentioned in the seventeenth century in *Museum Wormianum* (Worm 1655), although their true nature had not been recognized at that time. The first scientific collection and description of fossil plants from this locality date back to the eighteenth century when Eggert Ólafsson and Bjarni Pálsson explored Iceland on behalf of the Danish Royal Academy of Sciences (see Chap. 2). Fossils from the Brjánslækur-Seljá Formation were later described by Heer (1868), Windisch (1886a, b), Friedrich (1966), and Akhmetiev et al. (1978). Friedrich and Símonarson (1981) claimed that the Surtarbrandsgil gully at the Brjánslækur farm is the longest known and "most interesting" among all the plant localities in Iceland, and Mai collectively termed all Miocene plant localities from Iceland "Florenkomplex Brjánslaekur" (Mai 1995, p. 343). The same author pointed out that no equivalent forest type is known from the remaining Brito-Arctic Igneous Province, Western Europe or North America.

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DOI 10.1007/978-94-007-0372-8_5, © Springer Science+Business Media B.V. 2011

The Brjánslækur-Seljá Formation can be traced along the coastline of the southwestern part of the Northwest Peninsula. The formation is named after two outcrops where macrofossils are found in vast numbers, at the river Seljá in the Vaðalsdalur valley and the Surtarbrandsgil gully near the farm Brjánslækur (Fig. 5.1, Plate 5.1). Friedrich (1966) and Akhmetiev et al. (1978) emphasised the floristic affinities of the 12 Ma floras of Iceland with modern vegetation types of eastern North America and speculated that Iceland was initially colonized from North America. In addition, Friedrich (1966) and Mai (1995) pointed out the pioneer character of the flora from Surtarbrandsgil and other Miocene floras from Iceland as reflected in the presence of taxa such as *Comptonia*, *Acer*, *Populus*, *Salix*, *Sassafras*, and Betulaceae.

The present chapter describes the floras, vegetation types, and changing environments during the late Serravallian, using regional geology and macro- and microfossils (Table 5.1; Plates 5.1–5.27) from the 12 Ma sediments of Seljá in Vaðalsdalur and Surtarbrandsgil near Brjánslækur (Fig. 5.1). Differences in the composition and abundance of fossil taxa and in sediment type and structure between the outcrops and their bearing on diverse environments during the time of accumulation are evaluated. In addition, environmental changes in Iceland during the Middle Miocene are compared to changes observed in Arctic North America and Europe.

## 5.2 Geological Setting and Taphonomy

The age determination of the Brjánslækur-Seljá Formation is based on absolute age determination from McDougall et al. (1984) and palaeomagnetic measurements (Friedrich 1966; Grímsson 2007) correlated to the world Cainozoic magnetotimescale by Berggren et al. (1995). Sediments of the 12 Ma formation are found along the southern coastline of the Northwest Peninsula. The sediments and fossil floras described in this chapter are located on a small cape, delineated by the Barðaströnd coastline on its western side and Vatnsfjörður fjord on its eastern side (Fig. 5.1). On this cape, sediments can be traced up the Vaðalsdalur valley on the western side of Mount Blankur, Mount Hamarshyrna, Mount Kikafell, and Mount Þverfell, and in the Brjánslækur area on the eastern side of this mountain ridge. Although thick sediments are traceable for several kilometres, macrofossils have only been found at few outcrops. The most prominent are the Seljá outcrop (Plate 5.1), situated high up in the Vaðalsdalur valley, and the Surtarbrandsgil outcrop (Plate 5.1), northwest of the farm Brjánslækur (Fig. 5.1).

The clastic sedimentary rock succession in the Vaðalsdalur region is between 10 and 18 m thick. Most outcrops have varying sandstones (fine- to coarse-grained) or siltstones. At Seljá (Fig. 5.2), the lowest part of the succession is made up of conglomerates and coarse sandstones. The sandstone unit is just over a metre thick and is followed by finely laminated (<1 mm to 1 cm thick layers) siltstone, ca 5 m thick. The siltstones are dark coloured and rich in organic detritus. They are followed by a ca 3 m thick sandstone unit. The sandstones are fine- to coarse-grained, dark greyish in colour, and form 1–5 cm thick layers. Coarser sandstones and conglomerates

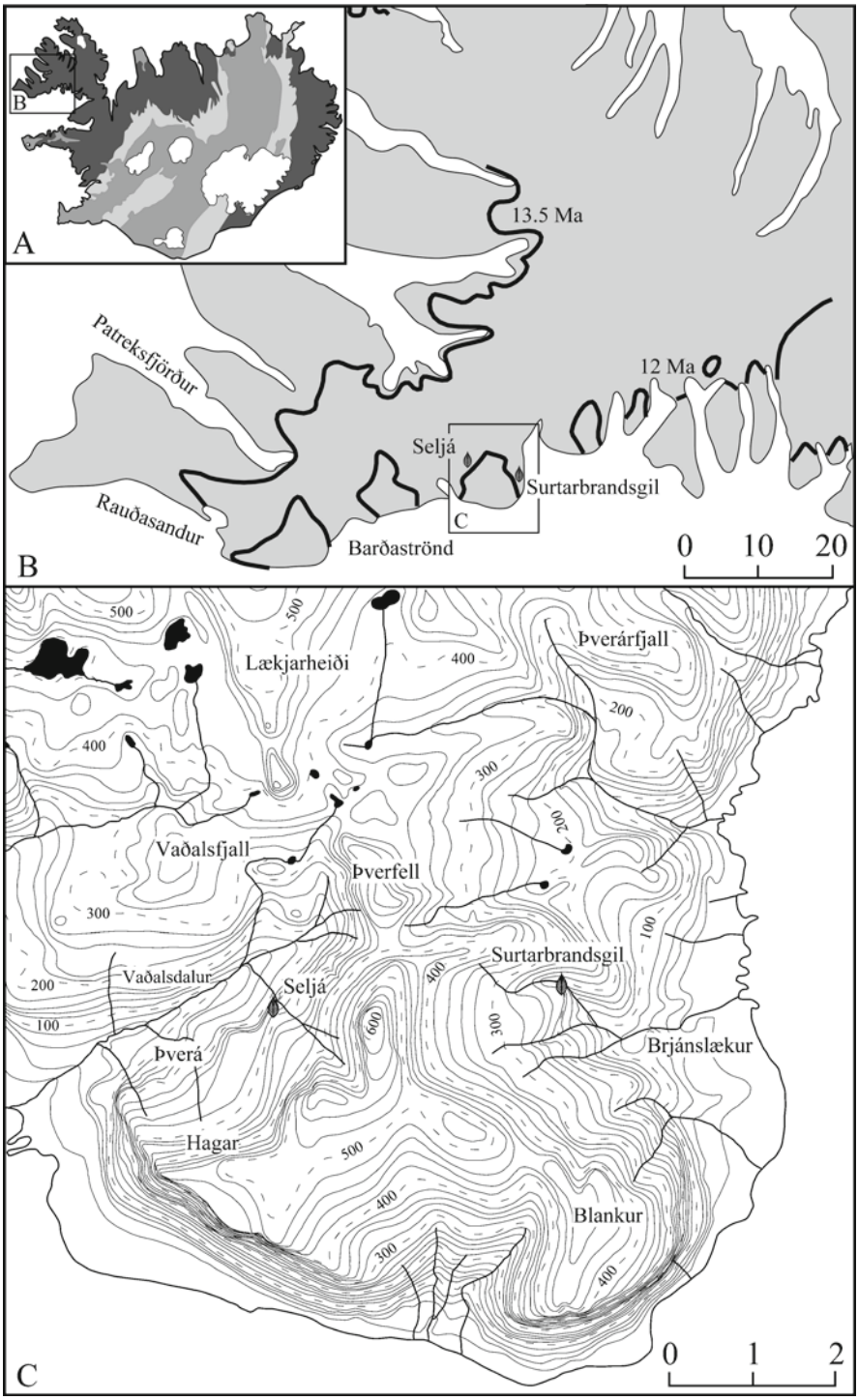



**Fig. 5.1** Map showing fossiliferous localities of the 12 Ma formation. **(a)** bedrock geology (see Fig. 1.10 for explanation), (**b**) extension of sedimentary rock formation, **(c)** Surtarbrandsgil and Seljá localities (geological background modified after Jóhannesson and Sæmundsson 1989; altitudinal lines from Landmælingar Íslands 1984). Scale bar in kilometres

**Table 5.1** Taxa recorded for the 12 Ma floras of Iceland

| Brjánslækur-Seljá Formation<br>Taxa | Pollen | Leaves | RP | Cuticle | DM |
|---|---|---|---|---|---|
| Bryophyta | | | | | |
| Hepaticae gen. et spec. indet. | + | | | | 1a |
| Lycopodiaceae | | | | | |
| *Lycopodium* sp. | + | | | | 1a |
| Equisetaceae | | | | | |
| *Equisetum* sp. | | + | | | 1a |
| Osmundaceae | | | | | |
| *Osmunda parschlugiana* | | **+** | | | 1a |
| Polypodiaceae | | | | | |
| Polypodiaceae gen. et spec. indet. 1 | + | | | | 1a |
| Polypodiaceae gen. et spec. indet. 2 | + | | | | 1a |
| Incertae sedis - unassigned spores | | | | | |
| Trilete spore fam. gen. et spec. indet. 1 | + | | | | 1a |
| Ephedraceae | | | | | |
| *Ephedra* sp. | + | | | | 1b |
| Cupressaceae incl. Taxodiaceae | | | | | |
| *Cryptomeria anglica* | | **+** | | **+** | 2a |
| Cupressaceae gen. et spec. indet. 2 (*Glyptostrobus* sp.) | + | | | | 2a |
| Cupressaceae gen. et spec. indet. 4 (*Sequoia* sp.) | + | | | | 2a |
| Pinaceae | | | | | |
| *Abies steenstrupiana* | + | + | **+ D** | | 2a |
| *Cathaya* sp. | + | + | | + | 2a |
| *Picea* sect. *Picea* | + | + | + D | | 2a |
| *Pinus* sp. 1 (Diploxylon type) | + | | | | |
| *Tsuga* sp. | + | + | | + | 2a |
| Sciadopityaceae | | | | | |
| *Sciadopitys* sp. | + | | | | 2a |
| Aquifoliaceae | | | | | |
| *Ilex* sp. 1 | + | | | | 1b |
| Betulaceae | | | | | |
| *Alnus cecropiifolia* | (+) | **+** | (+) D | | 1a, 2a |
| *Alnus gaudinii* | (+) | **+** | (+) D | **+** | 1a, 2a |
| *Betula islandica* | + | **+** | + D | | 1a |
| *Carpinus* sp. MT1 | (+) | + | (+) D | | 2a |
| *Carpinus* sp. MT2 | (+) | + | (+) D | | 2a |
| *Corylus* sp. | | + | | | 2b, 3 |
| Calycanthaceae | | | | | |
| aff. Calycanthaceae | + | + | | | 1b |
| Caprifoliaceae | | | | | |
| *Lonicera* sp. 1 | + | + | | | 1b |
| *Viburnum* sp. | + | | | | 1b |
| Cyperaceae | | | | | |
| Cyperaceae gen. et spec. indet. A | | + | | | 1b |

(continued)

**Table 5.1** (continued)

| Brjánslækur-Seljá Formation<br>Taxa | Pollen | Leaves | RP | Cuticle | DM |
|---|---|---|---|---|---|
| Ericaceae | | | | | |
| *Rhododendron* sp. 1 | + | | | | 1a, ?2a |
| ? *Rhododendron* sp. 2 | + | | | | 1a, ?2a |
| Juglandaceae | | | | | |
| *Carya* sp. | + | | | | 3, 2b |
| cf. *Juglans* | | + | | | 3, 2b |
| *Pterocarya* sp. | + | + | | | 2a |
| Lauraceae | | | | | |
| *Laurophyllum* sp. (*Laurus*) | | + | | | 1b |
| *Sassafras ferrettianum* | | **+** | | | 1b |
| Lemnaceae | | | | | |
| *Lemna* sp. | + | | | | 1b |
| Magnoliaceae | | | | | |
| *Liriodendron procaccinii* | | + | **+** D | | 1b, 2b |
| *Magnolia* sp. | | + | + D | | 1b |
| Myricaceae | | | | | |
| *Comptonia hesperia* | | **+** | | | 1b |
| Oleaceae | | | | | |
| cf. *Fraxinus* sp. | | | + D | | 2a |
| Platanaceae | | | | | |
| *Platanus* sp. | + | | | | 2a |
| Poaceae | | | | | |
| *Phragmites* sp. | | + | | | 1b |
| Rosaceae | | | | | |
| Rosaceae gen et. spec. indet. A | (+) | + | (+) D | | 1b |
| Rosaceae gen et. spec. indet. B | (+) | + | (+) D | | 1b |
| Rosaceae gen et. spec. indet. C | (+) | + | (+) D | | 1b |
| *Sanguisorba* sp. | + | | | | 1a |
| Salicaceae | | | | | |
| *Populus* sp. A (ex group *P. tremula* L.) | | + | + D | | 1a |
| *Salix gruberi* | + | **+** | | | 1a |
| Sapindaceae | | | | | |
| *Acer askelssonii* | (+)2 | + | **+** D | | 2a |
| *Acer crenatifolium* subsp. *islandicum* | (+)2 | **+** | **+** D | | 2a |
| Smilacaceae | | | | | |
| *Smilax* sp. | | + | | | 1b |
| Trochodendraceae | | | | | |
| *Tetracentron atlanticum* | **+** | | | | 2a |
| Ulmaceae | | | | | |
| aff. *Cedrelospermum* sp. | + | | | | 2a |
| *Ulmus* cf. *pyramidalis* | | **+** | | | 2a |
| Valerianaceae | | | | | |
| Valerianaceae gen. et spec. indet. | + | | | | 1a |

(continued)

**Table 5.1** (continued)

| Brjánslækur-Seljá Formation<br>Taxa | Pollen | Leaves | RP | Cuticle | DM |
|---|---|---|---|---|---|
| Incertae sedis - Magnoliophyta | | | | | |
| *Dicotylophyllum* sp. A | | + | | | ? |
| Pollen type 1 | + | | | | ? |
| Pollen type 2 | + | | | | ? |
| Pollen type 3 | + | | | | ? |
| Pollen type 4 | + | | | | ? |
| Pollen type 5 | + | | | | ? |
| Pollen type 6 | + | | | | ? |
| Pollen type 7 | + | | | | ? |

*L* leafy axis, *A* fruit attached to leafy axis, *D* fruit dispersed, *RP* reproductive structure, + organ present, **+** original description of species based on this organ, (+) organ belonging to genus but uncertain to which of the species, (+)2 indicating number of pollen types possibly belonging to the eponymous morphotaxon, *DM* dispersal mode: *1a* wind long distance (anemochory), *1b* bird long distance (endozoochory), *2a* wind short distance (anemochory), *2b* animals short distance (exozoochory), *3* dyschory

alternate with more fine-grained sandstones. A second siltstone unit overlies the sandstones but it is distinct from the lower one. The change from sandstone to siltstone is marked by intermixing units of sand- and siltstones. The siltstones are light coloured, brownish to yellowish, and poor in plant debris. Diatomite lenses become prominent in the upper part of the section. At the top of this section, diatoms become the main sediment type and a 20 cm thick diatomite bed contains the best preserved macrofossils (Fig. 5.2). Above the diatomite, a second compact sandstone unit follows. These sandstones are yellowish in colour and assorted with rhyolitic tephra (coarse tuffaceous sandstones). The lower part of this sandstone unit is cross-laminated. The sandstones are followed by a siltstone unit similar to the middle one. A distinct contact zone between the clastic sediments and the overlying volcanic mixture of pyroclastic, pillow and cube-jointed lava is visible (Fig. 5.2). There are also numerous ash and tephra layers in this section, mostly light-greenish in colour, but clearly with a high content of pumice fragments. The colour and structure are a result of alteration during the conversion of loose tephra to sedimentary rock.

Sediments in the Brjánslækur region are 8–20 m thick. The most interesting succession – in terms of plant macrofossils – is exposed in the Surtarbrandsgil gully (Plate 5.1). The sediments in this area differ slightly from those in Vaðalsdalur. Sandstones in the lowest part are followed by prominent homogeneous siltstones. The repeated sandstone units seen in Vaðalsdalur are not as distinct at this site. The lowest part of the succession in Surtarbrandsgil corresponds to the thin conglomerate bed and sandstones in Seljá (Fig. 5.2). Following the ca 3 m thick sandstone bed is an almost continuous siltstone unit towards the top. These siltstones are brownish in colour and correspond to the upper two siltstone units at Seljá. In Surtarbrandsgil, the siltstones contain thin layers of sandstones. These are both of clastic or erosional origin and reworked tephra layers (tuffs). In addition, several lignite lenses and layers occur within the siltstones. In the upper part of the Surtarbrandsgil succession, a diatomite bed similar to the one identified at Seljá is present. As at Seljá, a distinct contact

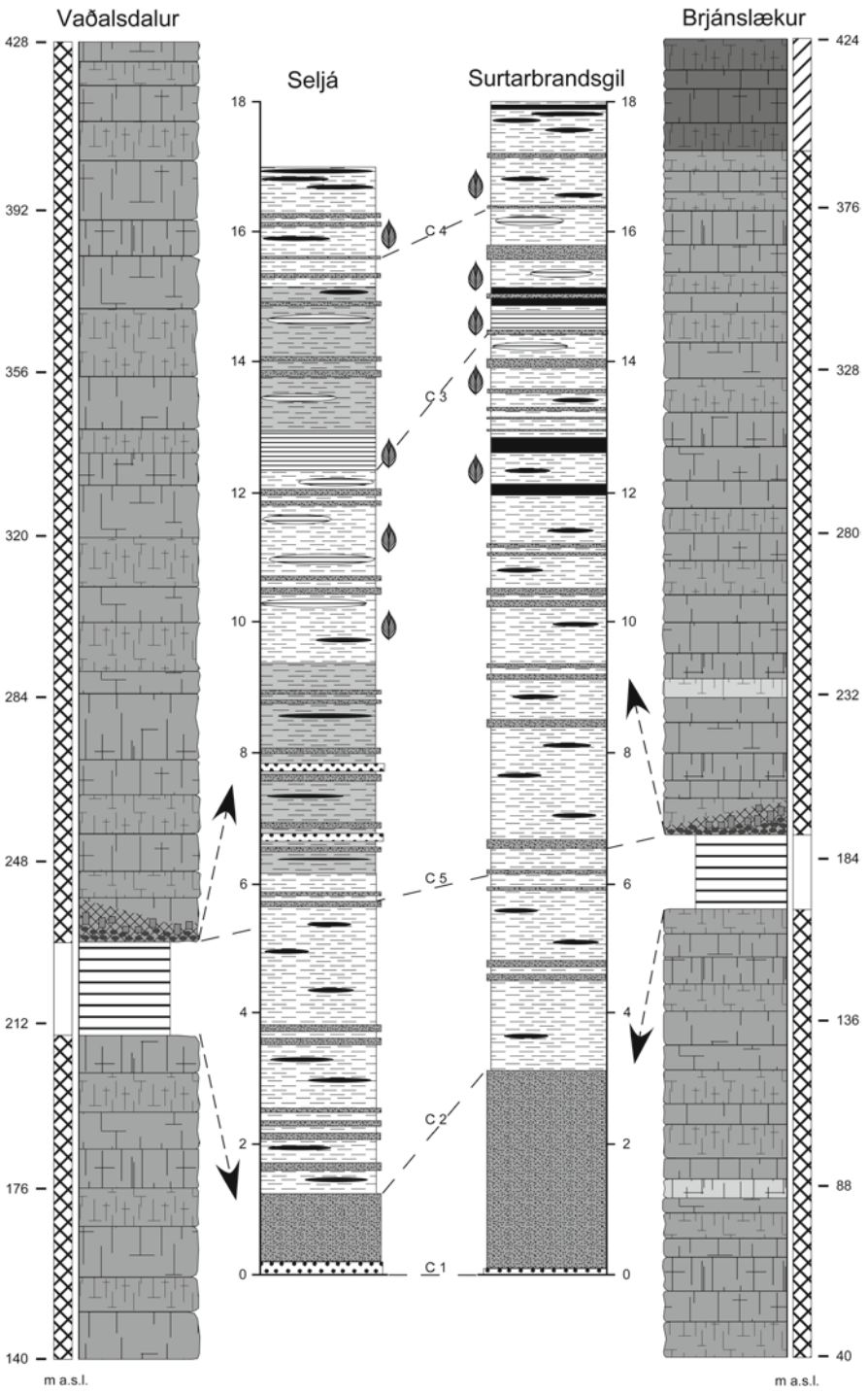



**Fig. 5.2** Generalized geological sections from Vaðalsdalur valley and the Brjánslækur region. Geological sections illustrate the sediments at Seljá and Surtarbrandsgil outcrops. C = correlation. *C1* lowest conglomerate, *C2* first sandstone unit, *C3* diatomite, *C4* triple ash layer, *C5* hyaloclastite

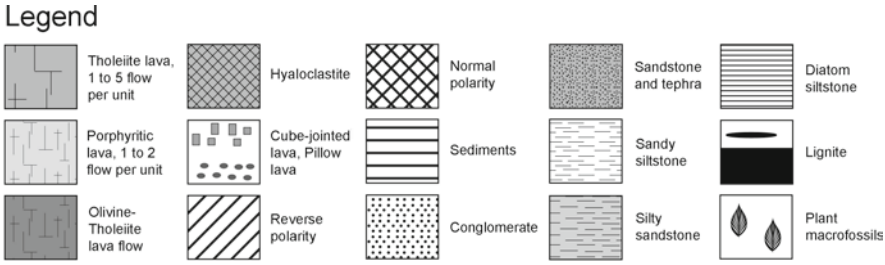



**Fig 5.2** (continued)

between the clastic sediments and overlying volcanic mixture of pyroclastics, pillow, and cube-jointed lava is seen in the Surtarbrandsgil succession (Fig. 5.2). Fossils are found in a lens up to 3 m thick and 25 m wide. In this lens, finely laminated siltstones with interlaminated diatomite are prominent (Fig. 5.2). The fine-grained sedimentary rocks split along the lamination and well-preserved plant fossils are found.

Fossils from Seljá are preserved as true impressions (Chaloner 1999) with no organic material present. Most of the fossils are reddish-brown leaf imprints in the fine-grained yellowish diatomite (Plate 5.1). In few instances, more robust organs such as catkins and fruits are preserved as lignified compressions. Plant fossils from Surtarbrandsgil show different preservation and are mostly cleavage impression-compressions (Chaloner 1999). When the fine-grained sediments at Surtarbrandsgil are split, a black lignite compression is present on the lower part and a white diatomite counterpart replica is on the upper part (Plate 5.1).

## 5.3 Floras and Vegetation Types

The Brjánslækur-Seljá Formation comprises a total of 65 taxa (Plates 5.1–5.27). Most taxa recorded (33) belong to woody angiosperms. Gymnosperms (mainly conifers and *Ephedra*) and ferns are represented by ten and eight taxa, respectively, while herbaceous angiosperms play a minor role (four taxa; Fig. 5.3). Macrofossils and pollen contribute more or less equally to the observed plant diversity (42 taxa represented by pollen, 35 by macrofossils). Twenty-eight taxa are documented by pollen only, and 15 by macrofossils only; 18 taxa are known from pollen and macrofossils. The macroflora of the Brjánslækur-Seljá Formation is the most diverse of all Cainozoic sediments of Iceland.

At Seljá, the fossil assemblage is dominated by foliage belonging to *Salix gruberi*, *Alnus cecropiifolia*, and *Populus* sp. (ex group *P. tremula*). Over 90% of the broad-leaved-type leaf fossils belong to one of these three types. *Salix* is the most common, followed by *Alnus* and *Populus*. *Phragmites* sp. and *Equisetum* sp. leaves and axes, and especially rhizomes, are frequently found and are characteristic for the lowest part of the diatomite bed. Other plant fossils identified as *Alnus* cf. *kefersteinii*, *Betula islandica*, *Carpinus* sp. 3 (bract), *Pterocarya* sp., *Magnolia* sp. 2, Rosaceae gen. et spec.

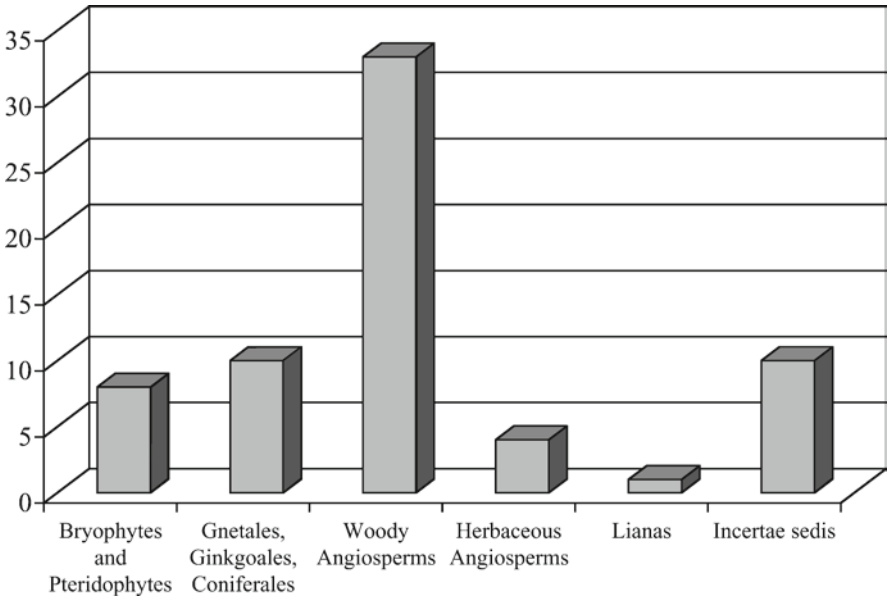



**Fig. 5.3** Distribution of life forms and higher taxa among the plants recovered from the 12 Ma sedimentary rock formation. Height of columns indicates number of taxa

indet. types A and D, *Populus* sp., and *Acer crenatifolium* subsp. *islandicum* are rare and only few specimens have been found. It is noteworthy that many taxa represented at Seljá by diaspores are known from leaves only or absent in Surtarbrandsgil (cones and catkins of *Alnus*, bracts of *Carpinus*, seeds of *Magnolia*, and catkins of *Populus*). This points to a species-poor oxbow lake situation at Seljá, with *Phragmites* in the littoral zone, and *Equisetum* in the undergrowth of a riparian *Salix*, *Alnus*, *Populus* stand. Rare remains of diaspores were blown in by wind or transported by water.

Most of the fossils from Surtarbrandsgil are leaves, but cones and cone scales are also found. Leaves of *Alnus cecropiifolia*, *Betula islandica*, and *Acer crenatifolium* subsp. *islandicum* are by far the most common types (Table 5.1). Other common elements belong to *Alnus gaudinii*, *Magnolia* sp. 1, *Sassafras ferrettianum*, and Rosaceae (type A). Among the more rare elements are *Laurophyllum* sp., *Comptonia hesperia*, and *Smilax* sp. Leaves of *Phragmites* are rarely found at this locality. Among gymnosperms, leafy axes of *Cryptomeria anglica* are most abundant, followed by various organ fossils of *Picea* section *Picea*. Ferns and fern allies are rarely found at Surtarbrandsgil, and only a few examples of *Equisetum* sp., and single specimens of *Osmunda parschlugiana* and *Dryopteris* sp. have been recorded. One layer is rich in leaf remains of conifer needles (*Cathaya*).

Many of the macrofossils found at Surtarbrandsgil and Seljá probably came from plants growing close to the sites of accumulation. The high amount of complete leaves in the Surtarbrandsgil sediments indicates short transport for many of the leaf types, suggesting that the place of origin was close to the accumulation site (autochthonous to semiautochthonous). Several of the more common plant fossils

from Surtarbrandsgil and Seljá, such as *Alnus*, *Betula*, *Salix*, *Populus*, and *Acer*, are today typical components of deciduous riparian forests along streams and rivers and at lake margins. The presence of *Phragmites* is also indicative of riparian vegetation. In contrast, compressions of branchlets of *Cryptomeria* are very abundant in the sediments from Surturbrandsgil, but occur in more coarse-grained, sandy layers that are devoid of angiosperm leaves. This suggests transport of *Cryptomeria* remains from upland forests.

Features such as buried stratovolcanoes and lava-filled valleys suggest that the palaeo-topography in Iceland was very similar to modern conditions. Today, the elevation of mountains in Iceland is limited to a maximum of ca 2,500 m a. s. l. by the strength of the oceanic crust beneath the island. This would imply that a complex landscape with a pronounced relief up to 2,000 m (stratovolcanoes) existed in the Miocene (Fig. 5.4). Iceland probably had vast lowlands that changed into highlands where volcanic mountains stood high up from their surroundings, and rivers and streams eroded canyons and valleys. Given the fact that sediments reflect different environments and that there was some altitudinal range in the region, the vegetation can be divided into wetland vegetation (aquatic vegetation, backswamp forests in Table 5.2); levée forests, well-drained lowland forests including lakeshore woodlands;

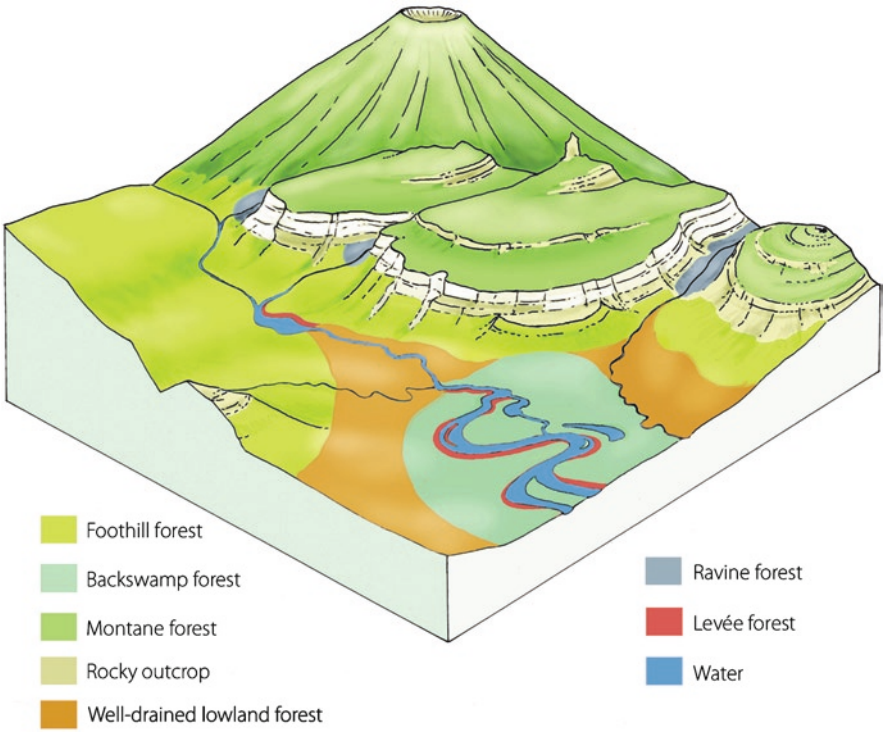



**Fig. 5.4** Schematic block diagram showing palaeo-landscape and vegetation types for the late Middle Miocene of Iceland. See Table 5.2 for species composition of vegetation types

**Table 5.2** Vegetation types and their components during the late Middle Miocene of Iceland

| Vegetation types 12 Ma | | | |
|---|---|---|---|
| **Aquatic vegetation** | *Lonicera* sp. 1 | **Rocky outcrop forests** | *Corylus* sp. |
| *Lemna* sp. | *Platanus* sp. | *Lycopodium* sp. | *Ilex* sp. |
| | *Pterocarya* sp. | *Ephedra* sp. | *Laurophyllum* sp. (*Laurus*) |
| **Backswamp forests and temporally flooded lake margin** | *Sassafras ferrettianum* | *Abies steenstrupiana* | *Liriodendron procaccinii* |
| | *Smilax* sp. | *Cathaya* sp. | *Lonicera* sp. 1 |
| *Osmunda parschlugiana* | | *Comptonia hesperia* | Rosaceae gen. et spec. indet. A |
| *Equisetum* sp. | **Well-drained lowland forests and lake margins** | *Picea* sect. *Picea* | Rosaceae gen. et spec. indet. B |
| *Glyptostrobus* sp. | *Hepaticae* gen. et spec. indet. | *Pinus* sp. 1 | Rosaceae gen. et spec. indet. C |
| *Alnus cecropiifolia* | *Osmunda parschlugiana* | *Sanguisorba* sp. | *Tetracentron atlanticum* |
| *Alnus gaudinii* | *Acer askelssonii* | *Tetracentron atlanticum* | *Ulmus* cf. *pyramidalis* |
| aff. Calycanthaceae | *Acer crenatifolium* subsp. *islandicum* | *Tsuga* sp. | |
| *Ilex* sp. | *Betula islandica* | | **Montane forests** |
| *Phragmites* sp. | aff. Calycanthaceae | **Foothill forests** | *Lycopodium* sp. |
| *Populus* (ex group *P. tremula*) | *Carpinus* sp. 1, sp. 2 | *Lycopodium* sp. | *Dryopteris* sp. |
| *Pterocarya* sp. | *Carya* sp. | *Polypodiaceae* gen. et spec. indet. 1, 2 | *Polypodiaceae* gen. et spec. indet. 1, 2 |
| *Salix gruberi* | aff. *Cedrelospermum* sp. | *Abies steenstrupiana* | *Abies steenstrupiana* |
| *Smilax* sp. | *Ilex* sp. | *Cathaya* sp. | *Cathaya* sp. |
| *Valerianaceae* gen. et spec. indet. | *Liriodendron procaccinii* | *Picea* sect. *Picea* | *Cryptomeria anglica* |
| *Viburnum* sp. | *Lonicera* sp. 1 | *Sequoia* sp. | *Picea* sect. *Picea* |
| | *Magnolia* sp. | *Tsuga* sp. | *Sciadopitys* sp. |
| **Levée forests and well-drained lake margins** | *Platanus* sp. | *Acer askelssonii* | *Tsuga* sp. |
| *Hepaticae* gen. et spec. indet. | *Pterocarya* sp. | *Acer crenatifolium* subsp. *islandicum* | *Fraxinus* sp. |
| *Lycopodium* sp. | Rosaceae gen. et spec. indet. A | | *Viburnum* sp. |
| *Polypodiaceae* gen. et spec. indet. 1, 2 | Rosaceae gen. et spec. indet. B | **Ravine forests** | |
| *Rhododendron* sp. 1 | Rosaceae gen. et spec. indet. C | aff. Calycanthaceae | |
| *Acer crenatifolium* subsp. *islandicum* | *Tetracentron atlanticum* | *Corylus* sp. | |
| *Carya* sp. | *Valerianaceae* gen. et spec. indet. | *Alnus cecropiifolia* | |
| *Viburnum* sp. | *Sassafras ferrettianum* | *Alnus gaudinii* | |
| *Rhododendron* sp. 2 | *Smilax* sp. | *Betula islandica* | |
| cf. *Juglans* | *Ulmus* cf. *pyramidalis* | *Carpinus* sp. 1, 2 | |
| *Liriodendron procaccinii* | *Viburnum* sp. | *Carya* sp. | |
| *Fraxinus* sp. | | aff. *Cedrelospermum* sp. | |
| **AZONAL VEGETATION** | | **ZONAL VEGETATION** | |

The palaeoecology of fossil species is reconstructed from their sedimentological context and ecology of modern analogues

and upland forests (foothill forests and montane forests in Table 5.2). In addition, some plants are indicative of rocky outcrop vegetation and ravine situations.

### 5.3.1 Wetland Vegetation

Plant remains associated with wetland vegetation (aquatic and swamp vegetation) belong to taxa that either float (*Lemna*) or grow in habitats with fluctuating ground water tables (Table 5.2). A number of taxa are typical elements of the littoral zone of a lake or backswamp forest composed of deciduous taxa (*Alnus*, *Populus*, *Pterocarya*, *Glyptostrobus*; Figs. 5.5 and 5.6) and a few evergreen shrubs (*Ilex*). Valerianaceae and *Osmunda* were part of the herb layer. *Smilax* was a liana growing in wetland forests and thickets as well as well-drained lowland forests. Periodically flooded areas were in close contact to well-drained forests.

### 5.3.2 Levée Forests, Well-Drained Lowland Forests Including Lakeshore Woodlands

A substantial part of the plant remains from the Brjánslækur-Selja Formation are representatives of relatively well-drained rich riparian forests composed of deciduous trees. Levée forests were rarely flooded and composed of fewer species tolerating high ground water tables, while more extensive and diverse woods behind lakeshores and riverbanks thrived on well-drained soils. These latter forests contained elements such as *Magnolia*, *Liriodendron*, *Sassafras*, and possibly *Platanus* (Fig. 5.6). In addition, trees from neighbouring vegetation types such as maples and Rosaceae were part of these forests. Therefore, these transitional woodlands became more varied with increasing distance from the waterline and gradually changed into more diverse mixed forests on mountain slopes (Fig. 5.4).

### 5.3.3 Upland Forests

Upland forests were rich mixed deciduous-evergreen broadleaved and conifer forests. Conifers formed a substantial part of the foothill forests (*Sequoia*, *Cryptomeria*, *Abies*, *Picea*, *Cathaya*, *Tsuga*) and the montane forests at higher elevations (also *Sciadopitys*). Large-leaved evergreen rhododendrons were elements of the undergrowth along with *Ilex*, *Lonicera*, *Viburnum*, and *Tetracentron*.

### 5.3.4 Other Vegetation Types

Two shrubs, *Comptonia* and *Ephedra* are at present typical elements of arid regions (Flora of North America Editorial Committee 1993, 1997). *Comptonia* comprises

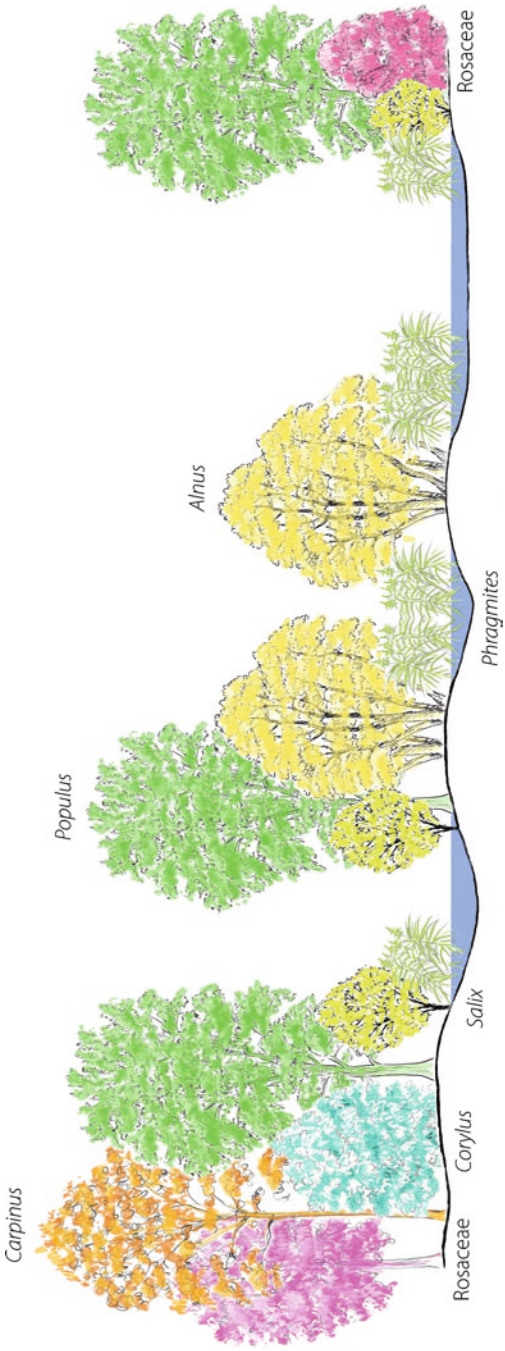



**Fig. 5.5** Schematic transect of a riparian forest with oxbow lakes and meandering river

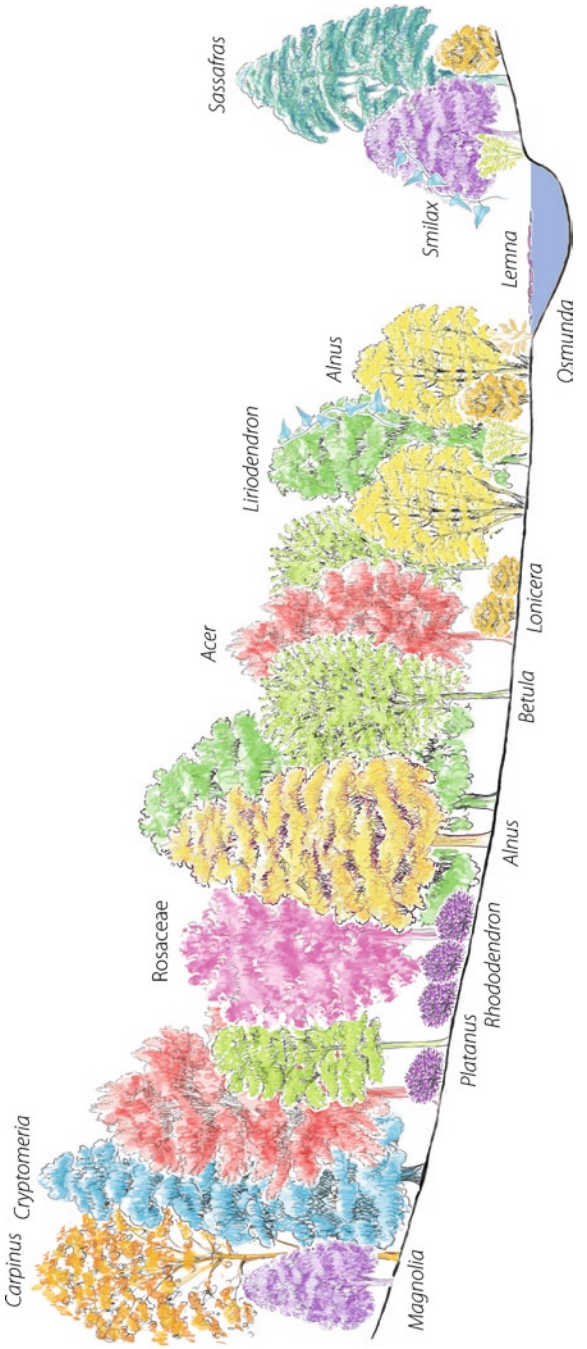



**Fig. 5.6** Schematic transect showing lake margin vegetation changing into well-drained lowland and foothill forest

only a single living species endemic to eastern North America where it grows on sandy and rocky substrates in pine forests, clearings or forest edges. *Ephedra* is found in Africa, Asia, Europe, North, and South America where it often occurs in dry areas but also in temperate regions. It displays a wide ecological range, growing on rocky substrates but also on flood lands. Overall, this may suggest that, in Iceland, these two elements could have inhabited rocky outcrop forests as well as sandy areas along rivers and shores.

## 5.4 Changing Environment

The continuous lava succession below the 12 Ma sedimentary formation suggests high and steady volcanic activity in the region prior to the accumulation of the plant-bearing sediments. Recent basalt lavas in Iceland originate from shield volcanoes or crater rows that are part of large volcanic systems. In the middle of such a system is a central volcano characterized by rhyolitic extrusive rocks (Saemundsson 1979). As the lavas around Vaðalsdalur and Brjánslækur are only basaltic, it is likely that the area was at some distance from a central volcano and that most lavas originated from fissure swarms at the outskirt of a volcanic system. The sediments suggest a sudden termination of lava formation in the region. At the same time, tephra (tuff) layers or pyroclastic beds in the sedimentary succession indicate the presence of an active central volcano. Thin and fine-grained ash layers (fine tuff) suggest relatively long distance origin, but other thick coarse-grained beds (coarse tuff) indicate a closer location to central volcanoes. In any case, it is clear that no lavas were formed during sedimentation, and erosion marked the surface of the uppermost lavas below the sediments. Accumulation of sediments started soon after the termination of lava formation and no apparent hiatus is present.

Sediments at Seljá and Surtarbrandsgil suggest that the region was a lowland and highland environment with extensive river systems and several small shallow lakes or ponds and swamps. The lowlands were surrounded by highland hillsides with valleys and volcanic mountains (Fig. 5.4). Initially, the substrate was affected by streams and rivers carrying clastic material from higher elevations to lowland areas. The landscape at Vaðalsdalur-Seljá was marked by streams with channels and deltas formed by meandering rivers running from the highlands towards the sea. After the initial erosion, the sediments became more fine-grained and lakes and ponds formed. As sediments kept accumulating in the area, deltas progressed over shallow lake sediments and fluvial sediments again became prominent. The lowland environment became dominated by a fully developed, complex river system with a surrounding floodplain, oxbow lakes, and swamps. At Brjánslækur-Surtarbrandsgil, a lake basin evolved in a high valley surrounded by hillsides and mountains.

In the Brjánslækur area, the palaeotopography is reflected by the varying thickness of the sediments at individual outcrops and the change in sedimentary type. Coarse-grained fluvial sediments are prominent in the beginning of the succession but finer grained sediments of lacustrine origin become more prominent in the

middle to upper parts. Initially, streams and rivers shaped the landscape in the Brjánslækur-Surtarbrandsgil region. The accumulation of coarse clastic sediments soon came to a stop and a lake environment became prominent, as reflected by fine clastic sediments and turbidity sandstones. Coarse tuff beds at Surtarbrandsgil indicate closer affinities to an active central volcano than at Seljá.

After some time of sedimentation, the whole clastic succession was overlain by a volcanic mixture of hyaloclastic pillow and cube-jointed lava. The thick hyaloclastite and the lava structures (pillow and cube) suggest an underwater eruption and/or lava running into water. The eruption was most likely along a fissure reaching into some of the lakes in the region of Vaðalsdalur and Brjánslækur. At this time, the region again became affected by volcanic activity, forming several lavas that overlay the sedimentary formation.

## 5.5 Ecological and Climatic Requirements of Some Modern Analogues

The following section provides information about the ecological and climatic properties of some modern analogues of the taxa present in the 12 Ma Brjánslækur-Seljá Formation. Fossil taxa are listed in Table 5.1; all potential modern analogues and their climatic requirements are provided in Appendix 13.1, Chap. 13. For brief descriptions of *Glyptostrobus*, *Sequoia*, and *Platanus*, see in Chap. 4, Sect. 4.4.

The monotypic genus *Cryptomeria* (Cupressaceae s. l.) occurs in southeast China to southern Central China and Japan at elevations from 800 to 2,500 m a. s. l. in its southern range and 50–1,600 m a. s. l. in its northern range (Flora of China Editorial Committee 1999; Iwatsuki et al. 2000). *Cryptomeria japonica* (Thunb. ex L. f.) D. Don forms part of humid well-drained mixed mesophytic forests sensu Wang (1961), and may occur in wet lowlands in Japan. It is a thermophilous species growing in a Cfa climate (warm temperate-humid-hot summer; Köppen and Geiger 1928; Kottek et al. 2006) with MAT 7–20.5°C.

*Sciadopitys* is a monotypic genus of southern Japan. *Sciadopitys verticillata* Sieb. and Zucc. occurs at elevations from 700 to 1,200 m a. s. l. (Iwatsuki et al. 2000) and is confined to cool-temperate, mixed evergreen-deciduous forest vegetation, often forming small pure stands. It is a temperate species growing in a Cfa to Dfb (snow, fully humid with warm summers; Köppen and Geiger 1928; Kottek et al. 2006) climate with MAT 7.4–16.6°C (MAT from Utescher and Mosbrugger 2009).

The fossil species *Alnus gaudinii* is morphologically very similar to the Caspian endemic *A. subcordata* C. A. Mey. and the Japanese *A. japonica* Sieb. and Zucc. *Alnus subcordata* occurs at elevations from 0 to 1,500 m a. s. l. in deciduous broad-leaved forests, and along streams. It thrives in a Cfa to Csa climate (Köppen and Geiger 1928; Kottek et al. 2006), with MAT 7.2–18.6°C. *Alnus japonica* has a vast distribution in East Asia, occurring in the Russian Far East, China, Korea, Japan, and Taiwan (Komarov 1970; Flora of China Editorial Committee 1999). It is an element of temperate forests, lake shores, and stream banks with an altitudinal

range from 0 to 1,500 m a. s. l. (Ohwi 1965). In accordance with its large distribution range, this species grows under a Cfa, Cwa (warm temperate, fully humid or winter dry, with hot summers), Dwa (snow, winter dry with hot summers), and Dwb climate (snow, winter dry with warm summers; Köppen and Geiger 1928; Kottek et al. 2006) with MAT 0.2–24.4°C.

The fossil *Betula islandica* falls within the variability of the modern section *Costatae* (Regel) Koehne based on its leaf size and type of fruit scales. Within the section *Costatae*, *B. islandica* shows similarities to the Eurasian species *B. utilis* D. Don and *B. ermanii* Cham. In addition, the unrelated (see Schenk et al. 2008) *B. papyrifera* Marshall has leaves that are fairly similar to *Betula islandica*. *Betula ermanii* is distributed in northeastern China, Japan, North Korea, and Russia (Kamchatka). It forms pure forest stands or is part of mixed coniferous and broad-leaved forests between 1,000 and 1,700 m a. s. l. *Betula utilis* has a range from Afghanistan, India, Nepal and Bhutan to temperate areas in western and Central China. This species grows in temperate broad-leaved forests at elevations between 2,500 and 3,800 m a. s. l. (Flora of China Editorial Committee 1999). *Betula papyrifera* is an element of rather moist forests on slopes or in swampy areas; it occurs from 300 to 900 m a. s. l. (Flora of North America Editorial Committee 1997). While *B. papyrifera* grows in Dfb and Dfc climates with MAT ranging from −12.2°C to 11.4°C (Thompson et al. 1999), *B. ermannii* and *B. utilis* thrive under winter dry Cwb and Dwa, Dwb, Dwc climates with MAT −7 to 14.6°C and −0.4 to 22.5°C, respectively.

*Sassafras* comprises only three species today displaying an East Asian-North American disjunction. *Sassafras tzumu* (Hemsl.) Hemsl. occurs in temperate and subtropical regions of China; it grows in light or dense forests from 100 to 1,900 m a. s. l. *Sassafras randaiense* (Hayata) Rehder is endemic to Taiwan and grows in evergreen broad-leaved forests between 900 and 2,400 m a. s. l. (Flora of China Editorial Committee 1999). *Sassafras albidum* (Nutt.) Nees occurs in eastern North America in temporally flooded to well-drained forests and disturbed areas from 0 to 1,500 m a. s. l. All three species are typical of a Cfa and Cfb climate with MAT from 6.7°C to 20.6°C (*S. albidum*) and 8.4–19.8°C (*S. tzumu*).

*Liriodendron* consists of only two modern species, *L. tulipifera* L. in North America and *L. chinensis* Sarg. in Central China. *Liriodendron tulipifera* is restricted to eastern North America where it is an element of rich woodlands, bluffs, low mountains, and hills (Flora of North America Editorial Committee 1997); it grows from 0 to 1,500 m a. s. l. under a Cfa climate with MAT from 4.4°C to 22°C (Thompson et al. 1999). *Liriodendron chinensis* is native to central and southern China, where it thrives under a Cfa climate with MAT from 11°C to 18°C. Oswald Heer (Heer 1868, pp. 70–71) previously used the fossil species *Liriodendron procaccinii* as a key taxon to estimate the climate of the Miocene in Iceland. He compared the fossil species to the modern *L. tulipifera* from eastern North America. Using the distribution limits of fruiting cultivated *L. tulipifera* in Europe, he concluded that the mean annual temperature (MAT) for Iceland was at least 11.5ºC during the Miocene.

*Comptonia peregrina* (L.) J. M. Coult. is another species endemic to eastern North America. It is a small shrub on dry, sandy to rocky substrates in pine forests,

clearings, or forest edges; it occurs from 0 to 1800 m a. s. l. with MAT from 3.4°C to 15.6°C (MAT from Utescher and Mosbrugger 2009). Its distribution range covers various climate types; warm temperate, fully humid, with hot or warm summers, i.e. Cfa and Cfb climates, to snow, fully humid, with hot and warm summers, i.e. Dfa and Dfb climates (Köppen and Geiger 1928; Kottek et al. 2006). During the Tertiary, *Comptonia* was a common element across the entire northern hemisphere which makes it difficult, based on a single living species, to draw conclusions about the ecological requirements of fossil representatives (Mai 1995).

Overall, both the macrofossil and the palynological records are suggestive of humid warm temperate conditions (Cfa climate) in the lowlands (*Glyptostrobus*, *Platanus, Sassafras*) and a slightly cooler climate in the uplands (Cfb climate). The temperature requirements (MAT) of the taxa encountered in the ca 12 Ma floras are between 9°C and 14°C for upland environments and up to ca 15°C for lowland riparian elements such as *Glyptostrobus* (Appendix 13.1, Chap. 13). Available evidence suggests that the climate was similar to the one estimated for the 15 Ma formation.

## 5.6 Taxonomic Affinities and Origin of the Middle Serravallian Floras

Most of the plant taxa recorded for the 12 Ma formation have related fossil species and potential modern analogues in all three northern temperate regions (Eastern Asia, Europe and Asia Minor, North America). For example, the genera *Sassafras* and *Liriodendron* that are restricted to the 12 Ma sedimentary rock formation in Iceland, occurred across the whole northern hemisphere during the Tertiary (Mai 1995; Manchester 1999) and display an East Asian-eastern North American disjunct distribution at present. Other taxa with a present northern hemisphere disjunct distribution that appear for the first time in the 12 Ma sedimentary formation in Iceland are, among others, *Acer askelssonii* (modern *Acer* section *Acer*), *A. crenatifolium* (modern *Acer* section *Rubra*; see Chap. 3), *Carya*, *Laurophyllum* (Lauraceae), *Corylus*, and *Lonicera*. One taxon, endemic to North America at present, *Comptonia*, is not indicative of floral affinities, since it was a widespread element in the European Tertiary (Mai 1995) and was possibly a component of high latitude floras until the Early Pliocene (Seward Peninsula, Alaska; Matthews and Ovenden 1990). In contrast, a small number of plant taxa are strong indicators for either migration from Eurasia or North America. Among conifers, *Cryptomeria* and *Sciadopitys* are restricted to East Asia at present but were widespread in the European Tertiary (Mai 1995; Manchester et al. 2009). Both genera have an ambiguous fossil record for North America (Aulenback and LePage 1998; Manchester et al. 2009; but see Matthews and Ovenden 1990, who reported *Sciadopitys* from the Pliocene of the Devon and Meighen islands). Overall, this points to a European rather than North American origin. The same may be true for *Alnus gaudinii* which is morphologically most similar to various Eurasian modern species and was a typical element of the European Tertiary (Kvaček et al. 2002; Denk et al. 2005).

## 5.7 Transitional Phase 15–12 Ma: Iceland, Arctic North America and Europe

From the Late Oligocene to the Middle Miocene (ca 27–15 Ma), a global warming trend reduced the Antarctic ice sheet and global ice volume remained low. This warm phase culminated in the Mid-Miocene Climatic Optimum (ca 17–15 Ma; Zachos et al. 2001) and was followed by gradual cooling associated with a re-establishment of the Antarctic ice sheet. This global trend has been recorded in various floras across the northern hemisphere. White et al. (1997) studied pollen and spore assemblages from the western part of Arctic North America covering the past 18 Ma. In these palynological records, a global warm peak ca 15 Ma (Seldovian Stage) is shown by the abundance of thermophilous taxa, including *Fagus* and *Quercus*. The subsequent Homerian Stage (13–8 Ma) is characterized by markedly cooler conditions reflected by the absence of warmth-loving taxa (Taxodiaceae-Cupressaceae-Taxaceae, Fagaceae, *Cercidiphyllum*, *Ilex*, *Nyssa*, *Liquidambar*, *Tilia*, *Acer*). The last occurrence of some warmth-loving taxa is recorded at 13.5 Ma, marked by a decline in the percentage of *Ulmus*-type pollen. The pattern of dramatic cooling after 15 Ma is congruent with the marine $\delta^{18}O$ decline and sea level fall after 14.8 Ma (Flower and Kennett 1994; Zachos et al. 2001).

A mid-latitude North American example for a late Middle to early Late Miocene flora is the Stinking Water flora from southeastern Oregon (Chaney and Axelrod 1959; K-Ar date 12–11 Ma, Armstrong et al. 1975; Appendix 5.1). Compared to the ca 15 Ma Clarkia flora (see Chap. 4), taxa belonging to Magnoliaceae and Lauraceae (*Magnolia*, *Liriodendron*, *Lindera*, *Persea*, and *Sassafras*) are present in the Clarkia flora but are absent from the younger Stinking Water flora. This may indicate regional floristic changes and extinction events across the time span 15–12 Ma. The Clarkia flora also comprises other warmth-loving elements such as *Diospyros* (Ebenaceae), *Gordonia* (Theaceae), *Gleditsia* (Fabaceae), and *Symplocos* (Symplocaceae) that have not been recorded for the Stinking Water flora. In addition, the Clarkia flora contains extinct taxa such as *Zizyphoides-Nordenskioldia*, *Palaeocarya*, and *Pseudofagus*, all missing in the Stinking Water flora. This could possibly indicate the extinction of these taxa in the region between 16–15 and 12 Ma.

In Iceland, no such conspicuous change as seen in the North American Arctic and partly mid-latitude floras across the transition 15–12 Ma can be observed. Taxodiaceae are abundant in the sedimentary rocks of the 12 Ma Brjánslækur-Seljá Formation and several warmth-loving angiosperms occur for the first time in the fossil record of Iceland (*Sassafras*, *Liriodendron*, *Laurophyllum*, *Dicotylophyllum* aff. *Neolitsea*) or persist from the 15 Ma Selárdalur-Botn Formation (*Magnolia*, *Platanus*). A possible explanation for this deviating pattern is given in Chap. 13.

For Europe, Kovar-Eder and Kvaček (2007) and Kovar-Eder et al. (2008) compared vegetation types for different time slices from which well-dated floras exist. For the time interval 17–14 Ma, subtropical broad-leaved evergreen forests and

partly subtropical subhumid xerophyllous forests are recorded for the western and southwestern parts of Europe. Warm temperate broad-leaved deciduous and partly mixed mesophytic forests dominated from the Carpathians eastwards. In general, broad-leaved evergreen forests had a wide north-south distribution, extending as far as Jutland (Denmark). In contrast, for the time interval 12–8.5 Ma, warm temperate broad-leaved deciduous forests and mixed mesophytic forests were characteristic of Central Europe and extended as far as Spain. At the same time, subtropical broad-leaved evergreen forests became much less common and were restricted to favourable regions. Kovar-Eder et al. (2008) state that the wide distribution of broad-leaved evergreen forests and mixed mesophytic forests during the period 17–14 Ma reflects the Mid-Miocene Climatic Optimum. The subsequent spread of mixed mesophytic and broad-leaved deciduous forests is directly linked to long-term cooling after 15 Ma. At the same time, a regional differentiation is seen for the period 17–14 Ma with warmer conditions in western and central Europe compared to cooler conditions further east. Humidity was lower in the western part of Europe (reflected by the higher proportion of sclerophyllous types and Fabaceae) but higher in the central and eastern regions. During the period 12–8.5 Ma, the climate was markedly cooler and more humid in large parts of Europe.

A rich flora that is similar in age to the Icelandic Surtarbrandur floras comes from eastern Ukraine (Krynka, Kryshtofovich and Baikovskaya 1965; part of "Florenkomplex Kosov-Krynka", Mai 1995). The late Badenian (ca 13 Ma) Krynka flora was dominated by broad-leaved deciduous taxa with a small component of evergreen elements (Magnoliaceae, Lauraceae, Ericaceae, *Buxus*, *Ilex*). Among the broad-leaved deciduous taxa, Fagaceae, Betulaceae, Rosaceae, and Sapindaceae (*Acer*) were most prominent, but Juglandaceae and Ulmaceae were also characteristic elements of this flora. An interesting (perhaps regional) feature of this and other eastern European floras of the Florenkomplex Kosov-Krynka is the complete lack of Cupressaceae (incl. Taxodiaceae) and Pinaceae (Mai 1995). While sharing a number of genera with the Icelandic floras, the Krynka flora contains various warmth-loving elements typical of mid-latitude floras across the northern hemisphere that never reached Iceland (Fabaceae, Rutaceae, Simarubaceae, Anacardiaceae, Nyssaceae and others; see Appendix 5.1). The late Sarmatian (ca 12–11.6 Ma) macroflora of Armavir (southwestern Russia; Kutuzkina 1964; Mai 1995) is geographically close to the Krynka flora and reflects broad-leaved deciduous vegetation that contained a number of warmth-lowing elements typical of mid-latitudes that never reached Iceland. Examples are Berberidaceae, Lauraceae (one single record in the Surtarbrandsgil locality), Fabaceae, and Hamamelidaceae. At the same time, a number of taxa found in the Armavir flora are also present in the 10, 12, and 15 Ma formations of Iceland. Examples are *Ginkgo*, *Cyclocarya*, *Platanus*, *Pterocarya*, and *Rhododendron ponticum* type. According to Kutuzkina (1964) the Armavir flora contains a number of "modern" Eastern Mediterranean-Caucasian and Submediterranean elements (*Periploca*, *Punica*, *Pyracantha coccinea*, *Cotinus coggyria*, *Ligustrum* sp.; Appendix 5.1). This may reflect environmental changes related to global cooling (and regionally drier conditions).

In a more regional study, Kvaček et al. (2006) examined the changes in vegetation and climate types over the time period 17–16 Ma to 12 Ma in the Central Paratethys. During the time interval 17–16 Ma, subtropical broad-leaved forests with a substantial proportion of evergreen elements were common in the western parts, whereas mixed mesophytic and broad-leaved deciduous forests were more common near the mountains in the northern and central parts of the Central Paratethys. A general cooling and more pronounced climatic gradient between the northern and southern parts of the Central Paratethys was observed for the 12 Ma time slice. This is in accordance with the pattern observed by Kovar-Eder and Kvaček (2007).

## 5.8 Summary

In this chapter, an updated list of plant taxa based on macrofossils, pollen and spores is provided for the 12 Ma Brjánslækur-Seljá Formation. The fossil flora of this period is the most exotic one recorded for the Miocene in Iceland and contains taxa such as *Ephedra*, *Liriodendron*, *Comptonia*, *Smilax*, *Laurophyllum* and warmth-loving elements from older floras (*Cathaya*, *Cryptomeria*, *Glyptostrobus*, *Sequoia*, *Magnolia*, *Platanus*). The vegetation was diverse with lowland riparian and well-drained forests and upland forests. *Ephedra*, *Comptonia* and herbaceous taxa such as *Sanguisorba* may have inhabited more open places on rocky substrates. Overall, the flora is a typical northern hemispheric Miocene flora. Elements that appear for the first time in the 12 Ma formation could have colonized Iceland both from the west and from the east. The palaeoclimate inferred from potential modern analogues was humid warm temperate and is best described as a Cfa (to Cfb) climate according to Köppen. Global ice volume had remained low during the Late Oligocene and Early Miocene. This warm phase peaked in the Mid-Miocene Climatic Optimum (ca 17–15 Ma) and was followed by cooling due to the reestablishment of the Antarctic ice sheet. While this global cooling trend is also seen in fossil floras of Arctic North America and Europe, in Iceland markedly warm conditions persisted until 12 Ma.

## Appendix 5.1

Floristic composition of the 12 Ma sedimentary formation of Iceland compared to contemporaneous northern hemispheric mid-latitude floras from North America and western Eurasia.

| **Brjánslækur-Seljá flora, Iceland [ca 65°31′ N 23°12′ W]** | |
|---|---|
| 12 Ma | |
| This study | |
| 3 | Equisetum sp. |
| 1 | Hepaticae gen. et spec. indet. |
| 1 | Lycopodium sp. |
| 1, 3 | Osmunda parschlugiana |
| 1 | Polypodiaceae gen. et spec. indet. 1 |
| 1 | Polypodiaceae gen. et spec. indet. 2 |
| 1 | Trilete spore fam. gen. et spec. indet. 1 |
| 1 | Ephedra sp. |
| 1-3 | Abies steenstrupiana |
| 1, 3 | Cathaya sp. |
| 1, 3 | Cryptomeria anglica |
| 1 | Glyptostrobus sp. |
| 1-3 | Picea sect. Picea |
| 1 | Pinus sp. 1 |
| 1 | Sciadopitys sp. |
| 1 | Sequoia sp. |
| 1, 3 | Tsuga sp. |
| 1-3 | Acer askelssonii |
| 1-3 | Acer crenatifolium subsp. islandicum |
| 1 | aff. Cedrelospermum sp. |
| 1-3 | Alnus cecropiifolia |
| 1-3 | Alnus gaudinii |
| 1-3 | Betula islandica |
| 1, 3 | aff. Calycanthaceae |
| 1-3 | Carpinus sp. MT1 |
| 1-3 | Carpinus sp. MT2 |
| 1 | Carya sp. |
| 2 | cf. Fraxinus sp. |
| 3 | cf. Juglans |
| 3 | Comptonia hesperia |
| 1, 3 | Corylus sp. |
| 1 | Cyperaceae gen. et spec. indet. A |
| 1 | Dicotylophyllum sp. A |
| 1 | Ilex sp. 1 |
| 3 | Laurophyllum sp. (Laurus) |
| 1 | Lemna sp. |
| 3 | Liriodendron procaccinii |
| 1, 3 | Lonicera sp. 1 |
| 3 | Magnolia sp. |
| 3 | Phragmites sp. |
| 1 | Platanus sp. |
| 1 | Pollen type 1 |
| 1 | Pollen type 2 |
| 1 | Pollen type 3 |
| 1 | Pollen type 4 |
| 1 | Pollen type 5 |
| 1 | Pollen type 6 |
| 1 | Pollen type 7 |
| 1, 2 | Populus sp. A (ex group P. tremula L.) |
| 1, 3 | Pterocarya sp. |
| 1 | Rhododendron sp. 1 |
| 1 | Rhododendron sp. 2 |
| 1, 3 | Rosaceae gen et. spec. indet. A |
| 1, 3 | Rosaceae gen et. spec. indet. B |
| 1, 3 | Rosaceae gen et. spec. indet. C |
| 1-3 | Salix gruberi |
| 1 | Sanguisorba sp. |
| 3 | Sassafras ferrettianum |
| 3 | Smilax sp. |
| 1 | Tetracentron atlanticum |
| 3 | Ulmus cf. pyramidalis |
| 1 | Valerianaceae gen. et spec. indet. |
| 1 | Viburnum sp. |

**Stinking Water flora [ca 44°N 118°W]**
12-11 Ma (K-Ar)
Chaney, 1959

| | |
|---|---|
| 1 | **Polypodiaceae** |
| 1 | **Ephedra sp.** |
| 1, 3 | **Abies chaneyi Mason** |
| 1 | Cedrus sp. |
| 1 | **Cupressaceae/Taxodiaceae/Taxaceae** |
| 3 | **Glyptostrobus oregonensis Brown** |
| 3 | Keteleeria heterophylloides (Berry) Brown |
| 1, 3 | **Picea lahontense MacGinitie** |
| 1, 3 | **Picea magna MacGinitie** |
| 1, 3 | **Picea sonomensis Axelrod** |
| 1, 3 | **Pinus harneyana Chaney** |
| 1 | **Tsuga sp.** |
| 1, 3 | **Acer bendirei Lesquereux** |
| 1, 3 | **Acer bolanderi Lesquereux** |
| 1, 3 | **Acer columbianum Chaney** |
| 1, 3 | **Acer minor Knowlton** |
| 1, 3 | **Acer oregonianum Knowlton** |
| 1, 3 | **Acer scottiae MacGinitie** |
| 3 | Ailanthus indiana (MacGinitie) Brown |
| 1, 3 | **Alnus harneyana Chaney** |
| 1, 3 | **Alnus hollandiana Jennings** |
| 1, 3 | **Alnus relatus (Knowlton) Brown** |
| 1 | **Asteraceae** |
| 1 | **Betula sp.** |
| 1 | **Carya sp.** |
| 1 | Caryophyllaceae/Chenopodiaceae |
| 3 | Cedrela trainii Arnold |
| 1 | Celtis sp. |
| 1 | **Corylus sp.** |
| 1 | **Ericaceae** |
| 1 | Fagus sp. |
| 1 | **Fraxinus sp.** |
| 3 | Gymnocladus dayana (Knowlton) Chaney |
| 3 | Hydrangea bendirei (Ward) Knowlton |
| 1 | **Juglans sp.** |
| 1 | Liquidambar sp. |
| 3 | Mahonia reticulata (MacGinitie) Brown |
| 3 | Mahonia simplex (Newberry) Arnold |
| 1 | Nyssa sp. |
| 1 | Onagraceae |
| 1 | Ostrya sp. |
| 1, 3 | **Platanus dissecta Lesquereux** |
| 3 | **Populus lindgreni Knowlton** |
| 1, 3 | Potamogeton parva Brown |
| 3 | Ptelea miocenica Berry |
| 1, 3 | **Pterocarya mixta (Knowlton) Brown** |
| 1, 3 | Quercus dayana Knowlton |
| 1, 3 | Quercus hannibali Dorf |
| 1, 3 | Quercus prelobata Condit |
| 1, 3 | Quercus pseudolyrata Lesquereux |
| 1, 3 | Quercus simulatea Knowlton |
| 3 | **Rosa harneyana Chaney** |
| 1, 3 | **Salix hesperia (Knowlton) Condit** |
| 1, 3 | **Salix succorensis Chaney** |
| 1, 3 | **Smilax magna Chaney** |
| 3 | Spiraea harneyana Chaney |
| 1, 3 | Typha lesquereuxi Cockerell |
| 1, 3 | **Ulmus speciosa Newberry** |

**Krynka flora [ca 47°30′ N 38°35′ E]**
Latest Badenian, "Presarmatian"
Kryshtofovich and Baikovskaya 1965; Mai 1995

| | |
|---|---|
| 3 | **Acer compositifolium Baik.** |
| 3 | **Acer pseudomiyabei Baik.** |
| 2, 3 | **Acer pseudoplatanus L.** |
| | **var. paucidentata Gaud.** |
| | **Acer sp.** |
| 3 | **Acer sp. cf. A. platanoides L.** |
| 2, 3 | **Acer subcampestre Goepp.** |
| | **var. acuminatolobatum Baik.** |
| 3 | **Acer subcampestre Goepp.** |
| | **var. integrilobifolium Baik.** |
| 3 | **Acer subcampestre Goepp.** |
| 3 | **var. macrophyllum Baik.** |
| 3 | Ailanthus confucii Ung. |
| 3 | **Alnus kefersteinii (Goepp.) Ung.** |
| 3 | **Alnus sp.** |
| 3 | Berberis longaepetiolata Baik. |
| 3 | **Betula grandifolia Ett.** |
| 2 | **Betula sp.** |
| 3 | **Betula tanaitica Baik.** |
| 3 | Bumelia sp. |
| 3 | Buxus pliocenica Sap. et Mar. |
| 2 | Carex sp. |
| 2 | **Carpinus cf. laxiflora Bl.** |
| 2, 3 | **Carpinus grandis Ung.** |
| 2 | **Carpinus marmaroschia Iljinskaja** |
| 3 | **Carya denticulata (Web.) Iljinskaja** |
| 3 | Celtis trachytica Ett. |
| 3 | Ceratophyllum sniatkovii Krysht. |
| 3 | Cercis turgaica Usnadze |
| 3 | Clerodendron ovalifolium Baik. |
| 3 | Clethra maximoviczii Nath. |
| 3 | Cornus attenuata Ett. |
| 3 | Cornus cf. acuminata Web. |
| 3 | Cornus megaphylla Hu et Chaney |
| 3 | Cornus oeningensis (Heer) Baik. |
| 3 | Cornus studeri Heer |
| 3 | **Corylus insignis Heer** |
| 3 | Cotoneaster sp. cf. C. andromedae Ung. |
| 3 | Crataegus praemonogyna Krysht. |
| 3 | Daphne limnophylla (Ung.) Baik. |
| 3 | Diospyros brachysepala A. Br. |
| 3 | Elaeagnus sp. |
| 3 | Eucommia palaeoulmoides Baik. |
| 3 | Fagus orientalis var. fossilis (Lipsky) Palibin |
| 2 | Fagus sp. |
| 2 | Genista sp. |
| 3 | Hibiscus splendens Baik. |
| 3 | Hovenia thunbergii (Nath.) Baik. |
| 3 | Hydrangea sp. |
| 3 | **Ilex falsanii Sap. et Mar.** |
| 3 | **Juglans zaisanica Iljinskaja** |
| 3 | Laburnum sp. |
| 3 | Laurocerasus sp. |
| 3 | Leguminosae sp. |
| 3 | Ligustrum vulgare L. var. fossile Palib. |
| 2 | Liquidambar sp. |
| 3 | **Lonicera sp. A** |
| 3 | **Lonicera sp. B** |
| 3 | Loranthus sp. |
| 3 | **Magnolia cf. M. dianae Ung.** |
| 3 | **Magnolia cuneifolia Baik.** |
| 3 | **Magnolia sp.** |
| 3 | Mespilus sp. |
| 2, 3 | Nyssa vertumnii Ung. |
| 2, 3 | Ostrya kryshtofovichii Baik. |
| 3 | Paliurus sp. |
| 3 | Parrotia pristina (Ett.) Stur |
| 3 | Photinia acuminata Baik. |
| 3 | Physocarpus sp. |
| 3 | Pistacia cf. P. miocenica Sap. |
| 3 | Polygonum ukrainicum Baik. |
| 3 | **Populus balsamoides Goepp.** |
| 3 | Prunus palaeocerasus Ett. |
| 3 | Pyracantha sp. |
| 3 | Pyrus sarmatica (Krysht.) Baik. |
| 3 | Quercus pseudocastanea Goepp. |
| 3 | Quercus pseudorobur Kov. |
| 3 | Quercus sp. A |
| 3 | Quercus sp. B |
| 2 | Ranunculus sp. |
| 3 | **Rhododendron megiston Ung.** |
| 3 | **Rhododendron sp.** |
| 3 | Rhus noeggerathii Weber |
| 3 | Rosa lignitum Engelhardt (non Heer) |
| 3 | Rubus palaeohirtus Baik. |
| 3 | **Salix media A. Braun** |
| 3 | Salvinia natanella Shap. |
| 3 | Sambucus palaeoracemosa Baik. |
| 3 | Sapindus cupanioides Ett. |
| 3 | **Sassafras ferretianum Massal.** |
| 3 | Schisandra sp. |
| 3 | Skimmia sp. |
| 3 | Spiraea sp. |
| 3 | Staphylea cf. pinnata L. |
| 3 | Styrax protoobassia (Nath.) Tanai et Onoe |
| 3 | Styrax pseudoofficinale Baik. |
| 3 | Styrax sp. |
| 2 | Tilia sp. |
| 3 | **Ulmus carpinoides Goepp.** |
| 3 | **Ulmus longifolia Ung.** |
| 2 | **Ulmus sp.** |
| 3 | Vaccinium pseudouliginosum Krysht. |
| 3 | Vitis praevinifera Sap. |
| 3 | Vitis sp. |
| 3 | Vitis subintegra Sap. |
| 3 | Zelkova ungeri Kov. |

| **Armavir flora [ca 45°00' N 41°07' E]**<br>Middle/Late Sarmatian<br>Kutuzkina 1964; Mai 1995 | |
|---|---|
| 3 | Pteridium sp. |
| 3 | Ginkgo adiantoides (Ung.) Heer |
| 2 | **Pinus sp.** |
| 3 | **Acer decipiens A. Br.** |
| 2 | **Acer sp.** |
| 3 | **Alnus kefersteinii (Goepp.) Ung.** |
| 3 | Amelanchier sp. cf. A. rotudifolia (Lam.) Dum.-Cours. |
| 3 | Berberis sp. |
| | **Betula sp.** |
| 3 | Bumelia sp. (cf. B. lanuginosa (Michx.) Pers.) |
| 3 | **Calycanthus sp. (cf. C. florida L.)** |
| 3 | **Carpinus grandis Ung.** |
| 3 | Carya serrifolia (Goepp.) Kräusel |
| 3 | Carya sp. |
| 3 | Castanea atavia Unger |
| 3 | Celastrus palibinii Kutuzk |
| 3 | Cercidiphyllum crenatum (Ung.) R. W. Brown |
| 3 | Cinnamomum cf. lanceolatum (Ung.) Heer |
| 3 | Cinnamomum polymorphum (A. Br.) Heer |
| 3 | Clematis sp. |
| 3 | Cornus cf. sanguinea L. |
| 3 | Cornus sp. |
| 3 | Corylus sp. |
| 3 | Cotinus coggygria Scop. |
| 3 | Cyclocarya cycloptera (Schlecht.) Iljinskaja |
| 3 | Diospyros brachysepala A. Br. |
| 3 | Fagus orientalis Lipsky fossilis Palibin |
| 3 | Fraxinus inaequalis Heer |
| 3 | Fraxinus grossidentata Laurent |
| 3 | Gleditsia allemanica Heer |
| 3 | Hamamelis miomollis Hu et Chaney |
| 3 | Juglans acuminata A. Br. |
| 3 | **Laurus sp.** |
| 3 | Leguminosites sp. |
| 3 | Ligustrum sp. (cf. L. vulgare L.) |
| 3 | Liquidambar europaea B. Br. |
| 3 | Liquidambar sp. |
| 3 | Loranthus palaeoeuropaeus Kutuzk |
| 3 | Myrica laevigata (Heer) Sap. |
| 3 | Myrica lignitum (Ung.) Sap. |
| 3 | Myrica palaeogale Pilar |
| 3 | Parrotia pristina Ett. |
| 3 | Periploca angustifolia Kutuzk. |
| 3 | Phragmites oeningensis A. Br. |
| 3 | Phyllites sp. |
| 3 | Phyllites sp. (cf. Ilex fargesii Franch.) |
| 3 | **Platanus lineariloba Kolak.** |
| 3 | Podogonium knorrii Heer |
| 3 | **Populus balsamoides Goepp.** |
| 3 | **Populus latior A. Br.** |
| 3 | **Prunus sp.** |
| 3 | **Pterocarya castaneifolia (Goepp.) Schlecht.** |
| 3 | Punica granatum L. |
| 3 | Pyracantha coccinea Roem. |
| 3 | Quercus castaneifolia C. A. Mey. var. fossilis |
| 3 | Quercus neriifolia A. Br. |
| 3 | Quercus pseudorobur Kov. |
| 3 | **Rhododendron sp. (cf. R. ponticum L.)** |
| 3 | Rhus blitum Sap. |
| 3 | Robinia regelii Heer |
| 3 | Rosa sp. |
| 3 | **Salix angusta A. Br.** |
| **2** | **Salix integra Goepp.** |
| **2** | **Salix varians Goepp.** |
| 2 | Typha latissima A. Br. |
| **2** | **Ulmus carpinoides Goepp.** |
| **2** | **Ulmus longifolia Ung.** |
| **2** | **Vaccinium protoarctostaphylos Kolak.** |
| 2 | Vitis sp. |
| 2 | Zelkova ungeri Kov. |
| 2 | Zizyphus sp. |

Boldface indicates that the genus is present in the Brjánslækur-Seljá Formation. Grey shading indicates that the genus is present in the older Selárdalur-Botn Formation (15 Ma). *1* based on pollen, spores; *2* based on leaves and/or fruit/seed fossils; *3* based on leaf fossils

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## Explanation of Plates

**Plate 5.1** **1–4**. Seljá in Vaðalsdalur, Northwest Iceland, Brjánslækur-Seljá Formation (ca 12 Ma). **1**. View of the Seljá outcrop, sediments on the right side of the stream. **2**. Clastic sediments, diatomite at the base, siltstones above. **3**. Detail of sandstones and ash layers. **4**. Fossils preserved as red rusty impressions in white diatomite. **5–8**. Surtarbrandsgil at Brjánslækur, Northwest Iceland, Brjánslækur-Seljá Formation (ca 12 Ma). **5**. A look down the gully Surtarbrandsgil, sediments in middle of photo. **6**. The Surtarbrandsgil outcrop, note person standing on the mid left for scale. **7**. Lake deposited sedimentary rocks, including diatomite rich siltstones and sandstones, and occasional ash layer. **8**. Fossils preserved as compressions, revealed as part and counterpart, with the black organic plant material on one part and a diatomite crust on the counterpart

**Plate 5.2** **1–3**. Trilete spore fam. gen. et spec. indet. 1. **1**. Spore in SEM, distal polar view. **2**. Detail of spore surface. **3**. Spore in LM, polar view. **4–6**. Polypodiaceae gen. et spec. indet. 2. **4**. Spore in SEM, equatorial view. **5**. Detail of spore surface. **6**. Spore in LM, equatorial view. **7–9**. Hepaticae gen. et spec. indet. **7**. Spore in SEM, proximal polar view showing trilete tetrad mark. **8**. Detail of spore surface. **9**. Spore in LM, proximal polar view. **10–12**. *Lycopodium* sp. **10**. Spore in SEM, distal polar view. **11**. Detail of spore surface. **12**. Spore in LM, distal polar view. **13–15**. *Lycopodium* sp. **13**. Spore in SEM, distal polar view. **14**. Detail of spore surface. **15**. Spore in LM, proximal polar view, showing trilete tetrad mark. **16–18**. Polypodiaceae gen. et spec. indet. 1. **16**. Spore in SEM, equatorial view. **17**. Detail of spore surface. **18**. Spore in LM, equatorial view. **19**. *Osmunda parschlugiana*, small pinna (IMNH 6)

**Plate 5.3** **1–3**. *Ephedra* sp. **1**. Pollen grain in SEM, polar view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, polar view. **4–6**. *Ephedra* sp. **4**. Pollen grain in SEM. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7–9**. Cupressaceae gen. et spec. indet. 2 (*Glyptostrobus* sp.). **7**. Pollen in SEM. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM. **10** and **11**. Cupressaceae gen. et spec. indet. 2 (*Glyptostrobus* sp.). **10**. Pollen grain in SEM, detail of surface. **11**. Pollen grain in LM. **12–14**. Cupressaceae gen. et spec. indet. 2 (*Glyptostrobus* sp.). **12**. Pollen grain in SEM. **13**. Detail of pollen grain surface. **14**. Pollen grain in LM

**Plate 5.4** **1**. *Cryptomeria anglica*, branched shoot with needle like leaves (S 093406). **2**. Detail of Fig. 1 showing leaf arrangement. **3**. *Cryptomeria anglica*, long shoot with shorter lateral shoots (IMNH 88-01). **4**. *Cryptomeria anglica*, epidermis in LM, epidermal tissue with densely spaced and irregularly oriented stomata (S 093948-A). **5**. *Cryptomeria anglica*, epidermis in LM, epidermal tissue with densely spaced and irregularly oriented stomata (S 093406). **6**. *Abies steenstrupiana*, cone scale (S 094057-2). **7**. *Abies steenstrupiana*, cone scale (IMNH 59). **8**. *Abies steenstrupiana*, winged seed (S 094013-2). **9**. *Abies steenstrupiana*, winged seed (S 094032-2). **10–12**. *Abies* sp. 1. **10**. Bisaccate pollen grain in SEM, oblique proximal polar view. **11**. Detail of corpus. **12**. Pollen grain in LM, polar view

**Plate 5.5** **1–3**. *Pinus* sp. 1. (Diploxylon type) **1**. Bisaccate pollen grain in SEM, distal polar view. **2**. Detail of pollen grain surface showing both saccus (lower right) and corpus (upper left). **3**. Bisaccate pollen grain in LM, distal polar view. **4**. *Cathaya* sp., numerous oblong needle-like leaves (IMNH 43). **5**. *Cathaya* sp., epidermis in LM, epidermal tissue consisting of narrow and oblong cells, stomata in rows (IMNH 43). **6**. *Cathaya* sp., epidermis in LM, epidermal tissue consisting of narrow and oblong cells (IMNH 43). **7**. *Cathaya* sp., epidermis in LM, epidermal tissue with stomata in rows (IMNH 43). **8**. *Cathaya* sp., epidermis in SEM, epidermal tissue consisting of narrow and oblong cells (IMNH 43). **9**. *Cathaya* sp., epidermis in SEM, epidermal tissue with stomata (IMNH 43)

**Plate 5.6** **1.** *Picea* sp., shoot with leaves (IMNH 175). **2**. *Picea* sp., shoot with raised scars (IMNH 130). **3**. *Picea* sect. *Picea* sp., female cone (IMNH org 6). **4**. *Picea* sect. *Picea* sp., female cone (S094048). **5**. *Picea* sect. *Picea* sp., female cone (S 094059). **6**. *Picea* sp., winged seed (IMNH). **7**. *Picea* sp., winged seed (S 094027-1). **8–10**. *Picea* sp. **8**. Bisaccate pollen in SEM, equatorial view. **9**. Detail of cappa. **10**. Pollen grain in LM, equatorial view

**Plate 5.7** **1–3**. *Sciadopitys* sp. **1**. Pollen grain in SEM, proximal polar view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, polar view. **4**. *Tsuga* sp., long shoot with leaves (GM 673). **5**. *Tsuga* sp., needle (S 094004-1). **6**. *Tsuga* sp., needle (S 093406-2). **7**. *Tsuga* sp., epidermis in LM, stomata in rows (S 094004-1). **8**. *Tsuga* sp., epidermis in LM, consisting of long and narrow cells and stomata in rows (S 093406-2). **9–11**. *Tsuga* sp. 1. Pollen grain in SEM, proximal polar view. **10**. Detail of pollen grain surface. **11**. Pollen grain in LM, polar view

**Plate 5.8** **1–3**. *Ilex* sp. 1. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4**. *Lonicera* sp., narrow elliptic leaf, base acute (S 093936). **5**. *Lonicera* sp., narrow elliptic leaf (IMNH). **6–8**. *Lonicera* sp. 1. **6**. Pollen grain in SEM. **7**. Detail of pollen grain surface. **8**. Pollen grain in LM. **9–11**. *Viburnum* sp. **9**. Pollen grain in LM, equatorial view. **10**. Detail of pollen grain surface. **11**. Pollen grain in LM, equatorial view. **12–14**. *Viburnum* sp. **12**. Pollen grain in SEM, polar view. **13**. Detail of pollen grain surface. **14**. Pollen grain in LM

**Plate 5.9** **1**. *Alnus cecropiifolia*, large wide elliptic leaf with round base (IMNH). **2**. *Alnus cecropiifolia*, large wide elliptic leaf with acute apex (IMNH). **3**. *Alnus* sp., male catkins (IMNH org 113-02). **4**. *Alnus cecropiifolia*, detail showing round base (IMNH 6729). **5**. *Alnus* sp., narrow-winged seed (IMNH 204). **6**. *Alnus kefersteinii*, female infructescense (IMNH org 120-01). **7**. *Alnus gaudinii*, large wide elliptic leaf (IMNH). **8**. *Alnus gaudinii*, medium sized ovate leaf (IMNH 50). **9**. *Alnus gaudinii*, large wide elliptic leaf with cordate base and a long petiole (S 087465). **10**. *Alnus gaudinii*, medium sized narrow elliptic leaf (IMNH 194). **11–13**. *Alnus* sp. 1. **11**. Pollen grain in LM, polar view. **12**. Pollen grain in SEM, polar view. **13**. Detail of pollen grain surface

**Plate 5.10** **1**. *Betula islandica*, medium sized leaf (S 087422). **2**. Detail of Fig. 1 showing venation and teeth in basal part. **3**. Detail of Fig. 1 showing venation and teeth in apical part. **4**. *Betula islandica*, wide elliptic leaf with cordate base (IMNH 94). **5**. *Betula islandica*, large wide elliptic leaf with cordate base and acute apex (IMNH). **6**. *Betula islandica*, large wide elliptic leaf with round base (IMNH 170-01). **7**. Detail of Fig. 6 showing venation and teeth along margin. **8**. *Betula islandica*, catkin scale with long lateral lobes (IMNH). **9**. *Betula islandica*, two catkin scales with long and narrow lobes (S 093963). **10**. *Betula islandica*, catkin scale (IMNH org 90). **11**. *Betula islandica*, catkin scale (IMNH 88-02). **12–14**. *Betula* sp. **12**. Pollen grain in SEM, polar view. **13**. Detail of pollen grain surface. **14**. Pollen grain in LM, polar view

**Plate 5.11** **1**. *Carpinus* sp. MT1, large wide elliptic leaf with asymmetric base (IMNH 166). **2**. Detail of Fig. 1 showing venation and teeth along margin. **3**. *Carpinus* sp. MT2, large narrow elliptic leaf with serrate margin (IMNH). **4**. *Carpinus* sp. MT2, small elliptic leaf with serrate margin (IMNH). **5**. *Carpinus* sp., winged fruit, partly preserved (IMNH 67812-06). **6** and **8**. *Carpinus* sp. 1. **6**. Pollen grain in LM, polar view. **8**. Pollen grain in SEM, polar view. **7, 9** and **10**. *Carpinus* sp. 1. **7**. Pollen grain in LM, polar view. **9**. Pollen grain in SEM, polar view. **10**. Detail of pollen grain surface. **11–13**. *Carpinus* sp. 1. **11**. Pollen grain in SEM, polar view. **12**. Detail of pollen grain surface. **13**. Pollen grain in M polar view

**Plate 5.12** **1**. *Corylus* sp., part of a large leaf (S 094065). **2**. Detail of Fig. 1 showing tertiary venation and teeth along margin. **3**. Detail of Fig. 1 showing veins entering teeth. **4–7**.

*Rhododendron* sp. 2. **4**. Tetrad in SEM. **5**. Detail of tetrad surface showing viscin threads. **6**. Tetrad in LM. **7**. Detail of tetrad surface showing microverrucae. **8–11**. *Rhododendron* sp. 1 (*R. ponticum* type). **8**. Tetrad in SEM. **9**. Tetrad in LM. **10**. Detail of tetrad surface showing oblong microrugulae. **11**. Detail of tetrad surface showing viscin thread

**Plate 5.13** **1–3**. *Carya* sp. **1**. Pollen grain in SEM, polar view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, polar view showing polar thinning. **4–6**. *Pterocarya* sp. **4**. Pollen grain in SEM, polar view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, polar view. **7–9**. *Lemna* sp. **7**. Pollen grain in SEM. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM. **10–12**. *Platanus* sp. **10**. Pollen grain in SEM, equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, equatorial view

**Plate 5.14** **1**. *Laurophyllum* sp. (*Laurus*), narrow elliptic leaf (S 094035-01). **2**. *Laurophyllum* sp. (*Laurus*), epidermis in LM, epidermal tissue with oil-cells (S 094035-01). **3**. *Sassafras ferrettianum*, medium sized 3 lobed leaf (IMNH). **4**. *Sassafras ferrettianum*, small elliptic leaf (IMNH 73-01). **5**. *Sassafras ferrettianum*, large wide elliptic/suborbiculate leaf (IMNH). **6**. *Sassafras ferrettianum*, large 3 lobed leaf (IMNH org 107)

**Plate 5.15** **1**. *Liriodendron procaccinii*, small 4 lobed leaf (GM 6790). **2**. *Liriodendron procaccinii*, part of a large 4 lobed leaf (IMNH 4787). **3**. *Liriodendron procaccinii*, samaroid fruit (S 094043-02). **4**. *Magnolia* sp., small narrow elliptic leaf (S 094018). **5**. *Magnolia* sp., medium sized narrow elliptic leaf with (IMNH 111-03). **6**. *Magnolia* sp., large leaf with entire margin (IMNH 117-01). **7**. *Magnolia* sp., seed (IMNH org 120-02). **8**. *Magnolia* sp., epidermis in LM, epidermal tissue consisting of undulate cells (S 094068)

**Plate 5.16** **1**. *Comptonia hesperia*, medium sized lobed leaf (S 134428). **2**. Detail of Fig. 1 showing lobes. **3**. *Comptonia hesperia*, small lobed leaf (IMNH). **4**. *Comptonia hesperia*, basal part of leaf (S 094066-02). **5**. Detail of Fig. 4 showing venation into lobes. **6**. cf. *Fraxinus* sp, samara (IMNH 54-02). **7**. Cyperaceae gen. et spec. indet. A, fragment of leaf (IMNH 6745-06A). **8**. Cyperaceae gen. et spec. indet. A, fragment of leaf (IMNH 6745-06B). **9**. *Phragmites* sp. **10**. *Phragmites* sp

**Plate 5.17** **1**. Rosaceae gen. et spec. indet. A, medium sized elliptic leaf (IMNH 66). **2**. Rosaceae gen. et spec. indet. A, part of small leaf, (S 134378-01). **3**. Detail of Fig. 2 showing venation and teeth along margin. **4**. Rosaceae gen. et spec. indet. B, large elliptic leaf with cordate base (S 094044-01). **5**. Rosaceae gen. et spec. indet. C, large elliptic leaf with obtuse base (S 093734). **6**. Detail of Fig. 5 showing venation and teeth along margin. **7**. Detail of Fig. 1 showing venation and teeth along margin. **8**. Rosaceae, gen. et spec. indet. B (IMNH). **9**. cf. Rosaceae, small fruit with the remnants of a calyx (S 134357)

**Plate 5.18** **1–3**. Rosaceae gen. et spec. indet. 3. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4–6**. Rosaceae gen. et spec. indet. 3. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7–9**. *Sanguisorba* sp. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view. **10–12**. *Sanguisorba* sp. **10**. Pollen grain in SEM, equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, equatorial view

**Plate 5.19** **1**. *Populus* sp. A (ex group *P. tremula* L.), large suborbiculate leaf with a long petiole (IMNH 6719-01). **2**. *Populus* sp. A (ex group *P. tremula* L.), large suborbiculate leaf with a long petiole (S 134363). **3**. *Salix gruberi*, narrow elliptic leaf (IMNH). **4**. *Salix gruberi*, narrow elliptic leaf with petiole (S 134360). **5**. *Salix gruberi*, elliptic leaf (S 134358). **6**. Detail of Fig. 5 showing venation and teeth along margin. **7–10**. *Salix* sp. 2. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Detail of pollen grain surface. **10**. Pollen grain in LM, equatorial view

**Plate 5.20** **1**. *Acer askelssonii*, medium sized 3 lobed leaf (IMNH 176). **2**. *Acer askelssonii*, large samara (IMNH org 106). **3**. *Acer crenatifolium* subsp. *islandicum*, small 3 lobed leaf (IMNH). **4**. *Acer crenatifolium* subsp. *islandicum*, small 3 (5) lobed leaf (IMNH). **5**. *Acer crenatifolium* subsp. *islandicum*, samaras (IMNH). **6**. *Acer crenatifolium* subsp. *islandicum*, samaras (IMNH 32). **7**. *Acer crenatifolium* subsp. *islandicum*, samara (IMNH 91)

**Plate 5.21** **1–3**. *Acer* sp. 3. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4–6**. *Acer* sp. 3. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7–9**. *Acer* sp. 2. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view

**Plate 5.22** **1**. *Smilax* sp., lower part of leaf (S 093953). **2**. Detail of Fig. 1 showing venation. **3**. *Ulmus* cf. *pyramidalis*, narrow elliptic leaf with forking secondary veins (IMNH). **4**. *Ulmus* cf. *pyramidalis*, large elliptic leaf with forking secondary veins (S093964). **5**. *Ulmus* cf. *pyramidalis*, small wide leaf (IMNH). **6**. *Ulmus* cf. *pyramidalis*, small ovate leaf (IMNH). **7**. *Ulmus* cf. *pyramidalis*, small ovate leaf (IMNH). **8–10**. aff. *Cedrelospermum* sp. **8**. Pollen grain in SEM. **9**. Detail of pollen grain surface. **10**. Pollen grain in LM

**Plate 5.23** **1–3**. *Tetracentron atlanticum*. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4–6**. *Tetracentron atlanticum*. Pollen gain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7–9**. *Tetracentron atlanticum*. **7**. Pollen grain in SEM, oblique view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, oblique view. **10–12**. *Tetracentron atlanticum*. **10**. Pollen grain in SEM, oblique polar view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, oblique polar view. **13–15**. Valerianaceae gen. et spec. indet. **13**. Pollen grain in SEM, Equatorial view. **14**. Detail of pollen grain surface. **15**. Pollen grain in LM, equatorial view

**Plate 5.24** **1**. aff. Calycanthaceae, large leaf with obtuse base (IMNH 98-01). **2**. aff. Calycanthaceae, small elliptic leaf (IMNH 64-03). **3**. aff. Calycanthaceae, small elliptic leaf with acute base (S 093977). **4**. Dicotylophyllum sp. A, leaf fragment (S 094061)

**Plate 5.25** **1–3**. Pollen type 1. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4–6**. Pollen type 1. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7–9**. Pollen type 2. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view. **10–12**. Pollen type 2. **10**. Pollen grain in SEM, equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, equatorial view

**Plate 5.26** **1–3**. Pollen type 3. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4–6**. Pollen type 4. **4**. Pollen grain in SEM. **5**. Detail of pollen surface. **6**. Pollen grain in LM. **7–9**. Pollen type 5. **7**. Pollen grain in SEM. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM. **10–12**. Pollen type 6. **10**. Pollen grain in SEM. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM

**Plate 5.27** **1–3**. Pollen type 7. **1**. Pollen grain in SEM. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM. **4–6**. aff. Calycanthaceae **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7–9**. aff. Calycanthaceae **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view. **10–12**. aff. Calycanthaceae **10**. Pollen grain in SEM, equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, equatorial view

## Plates

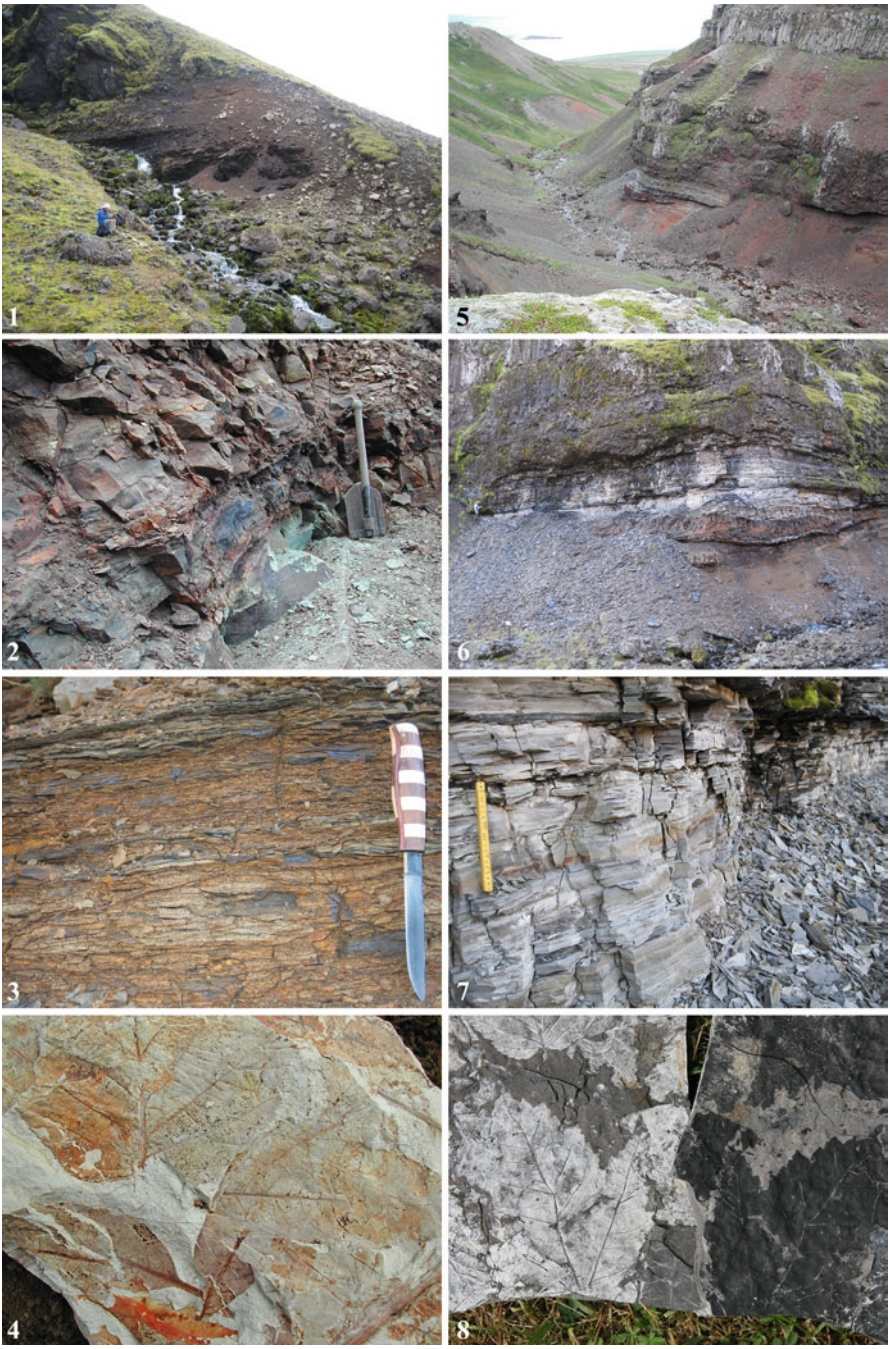



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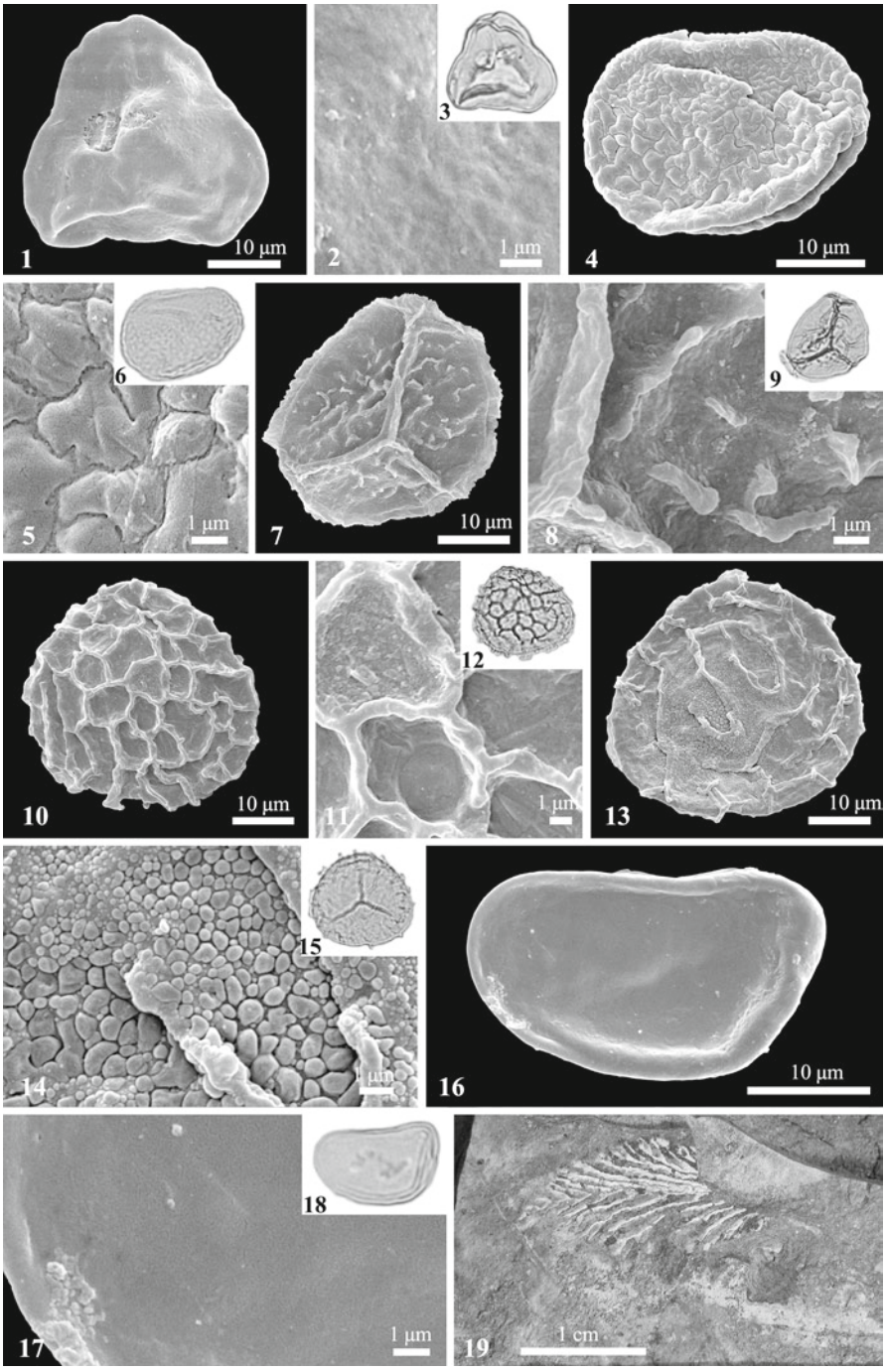

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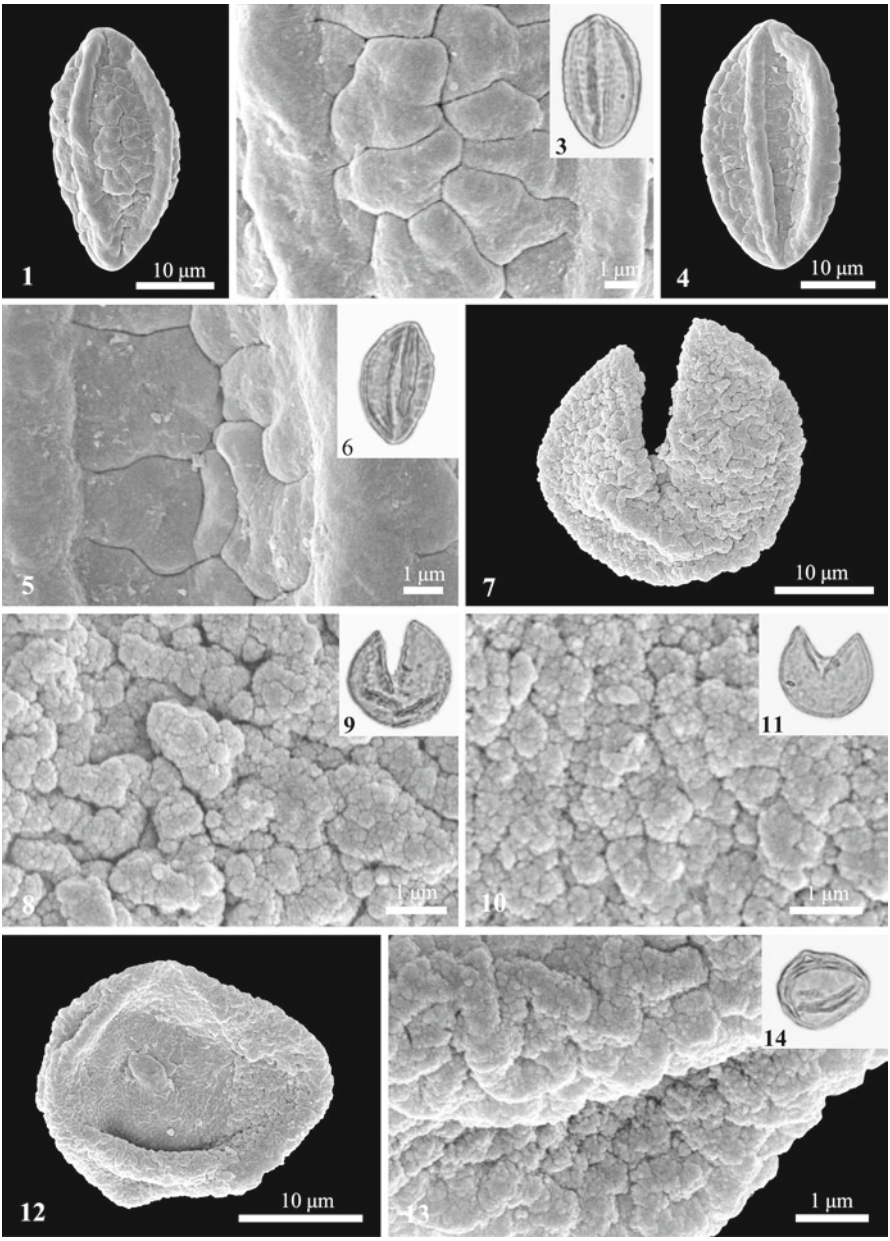

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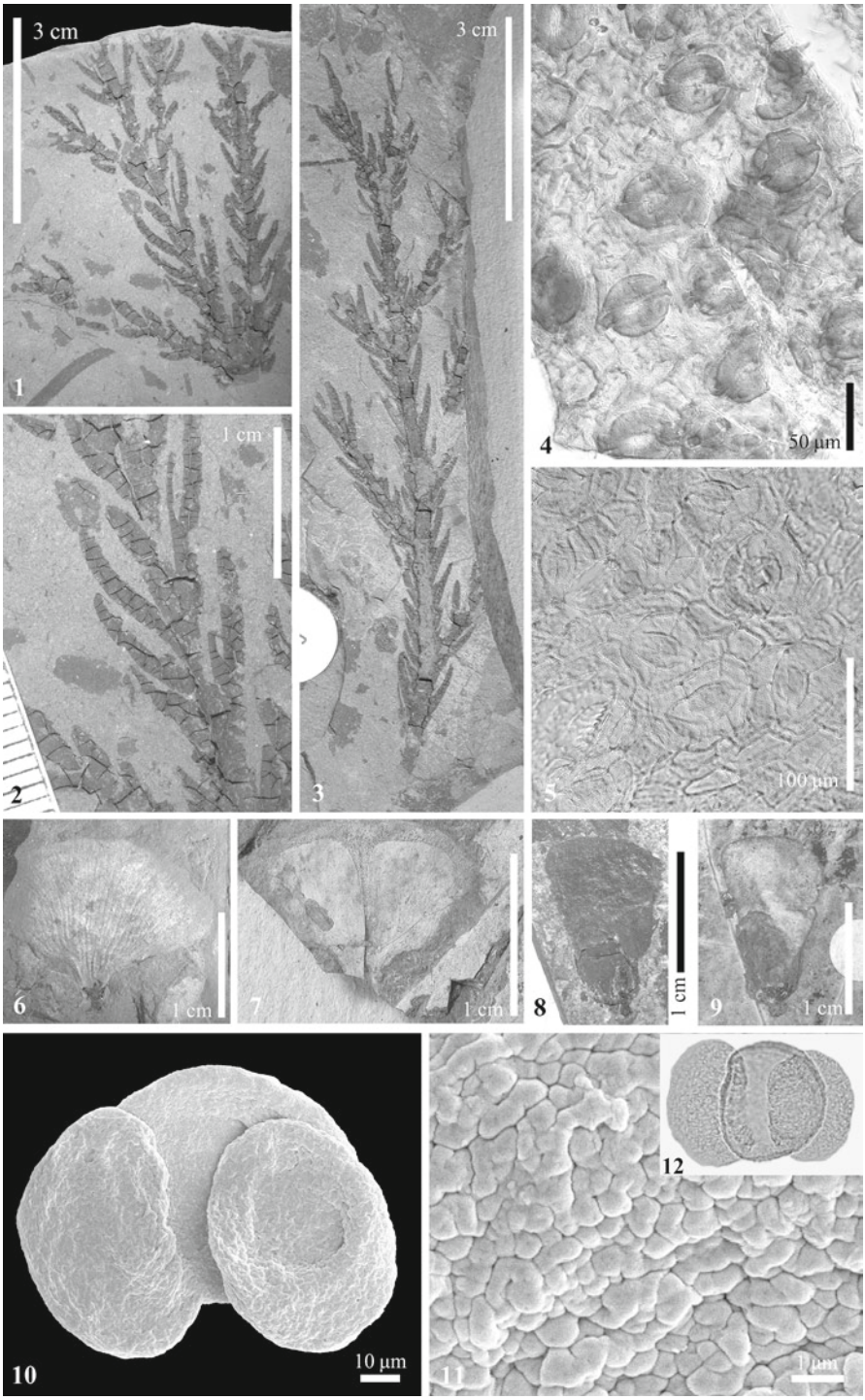

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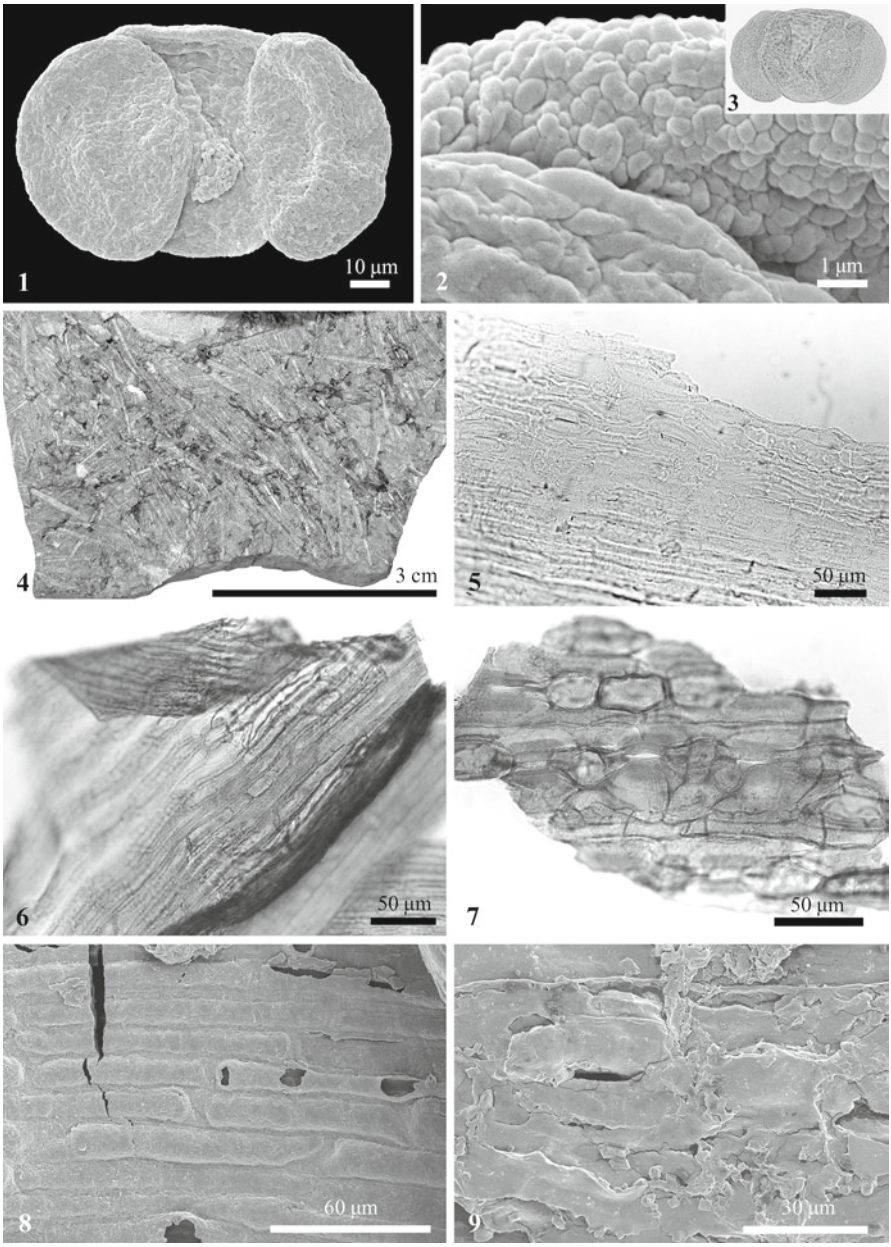



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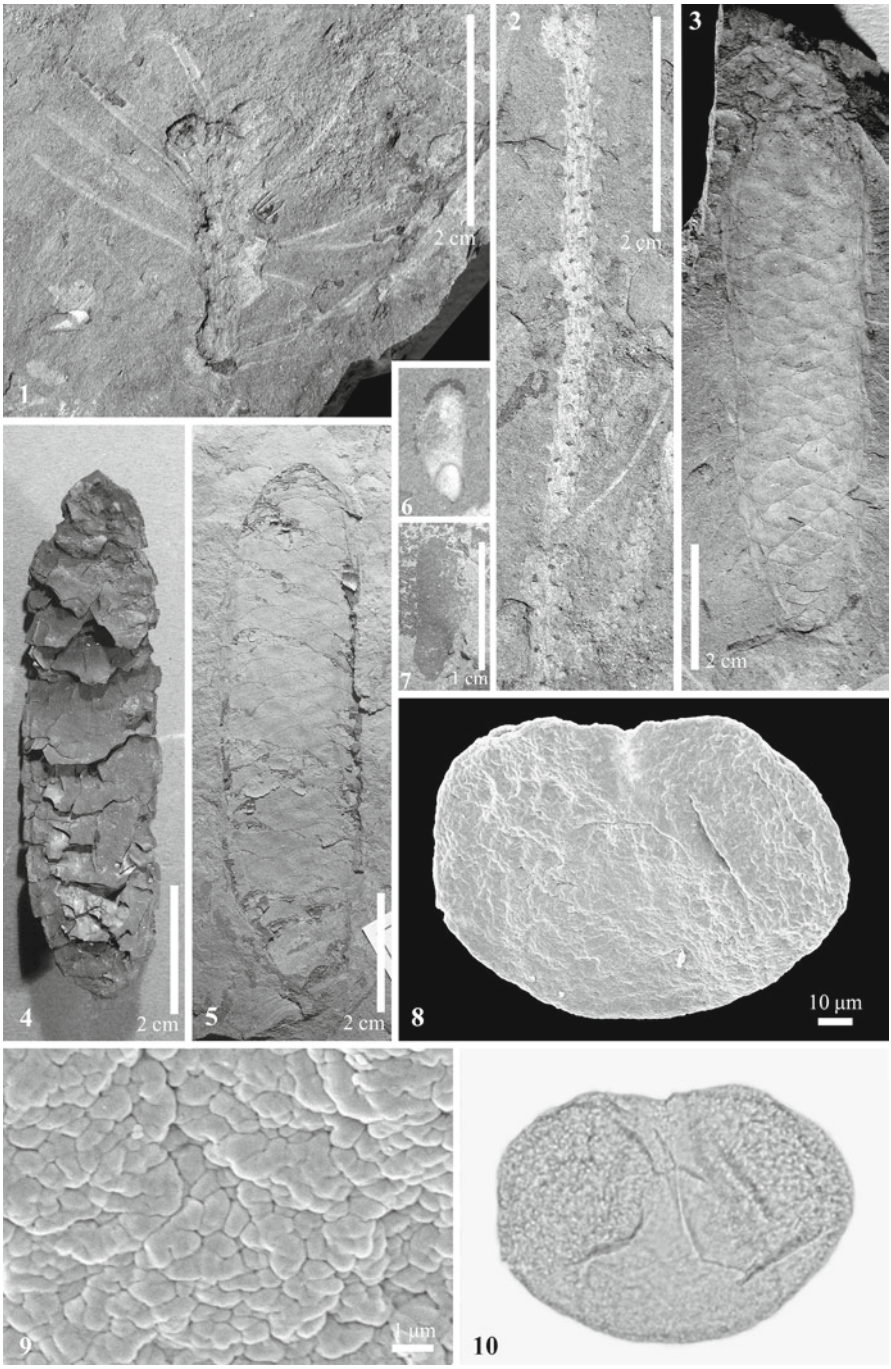



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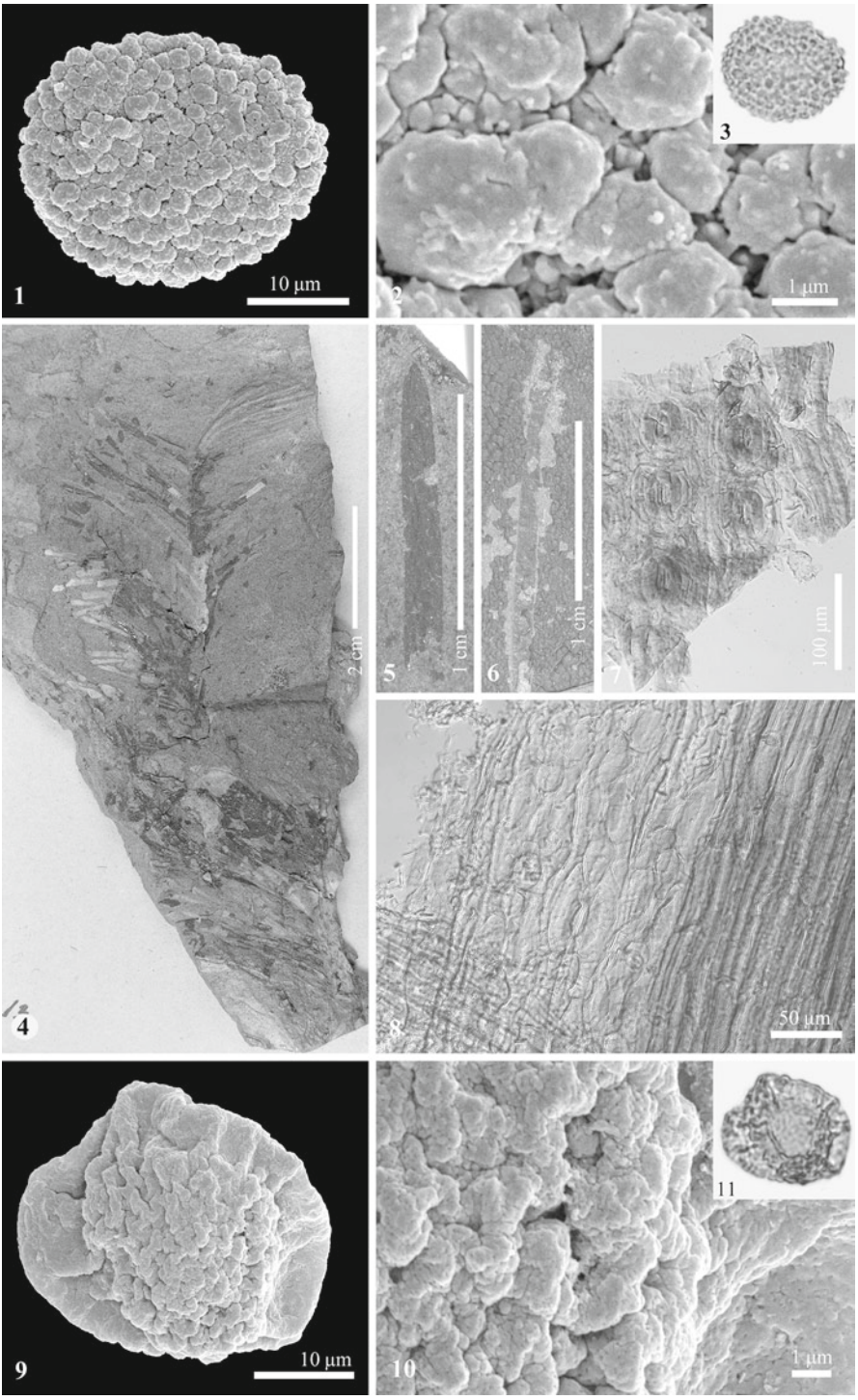



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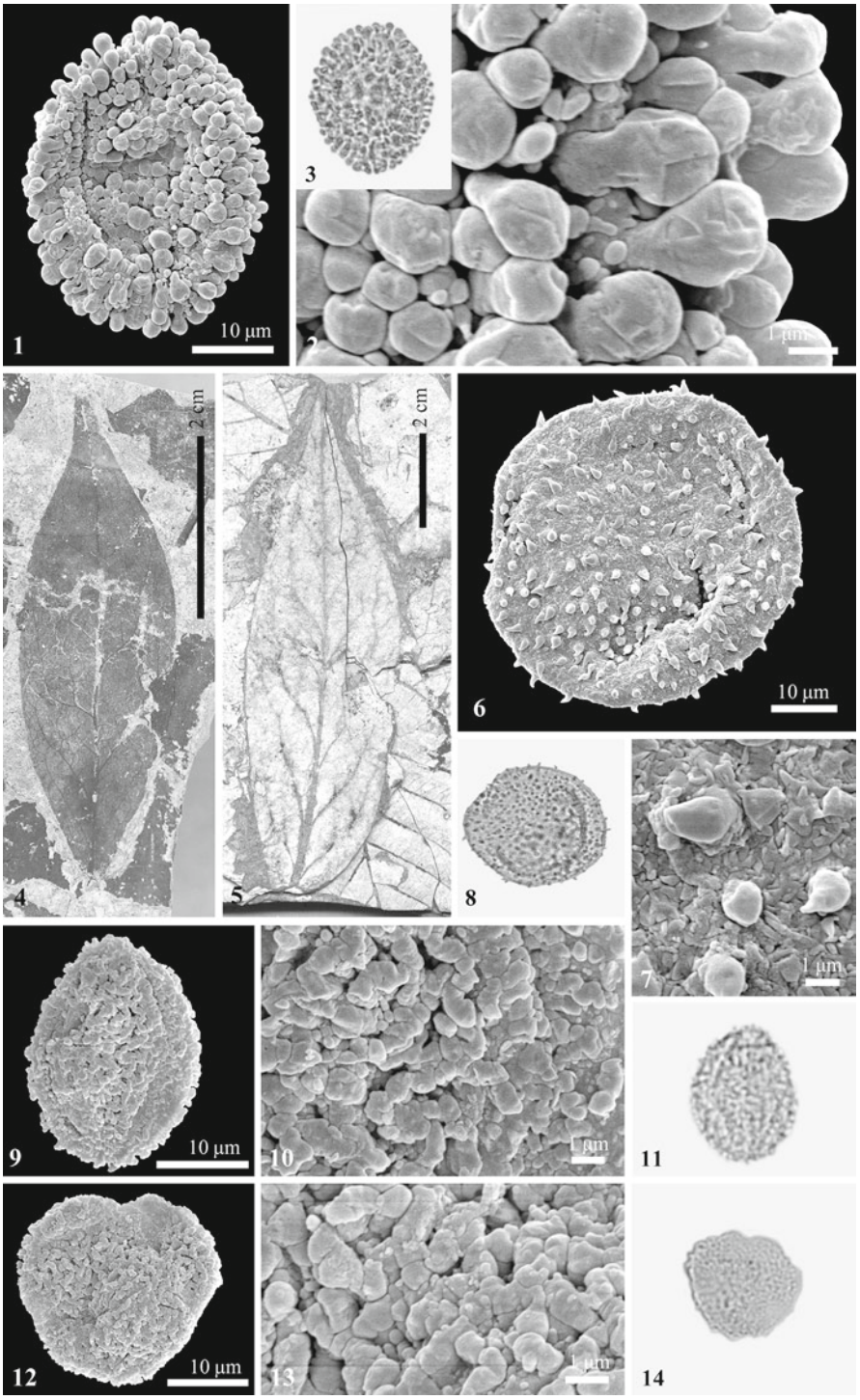

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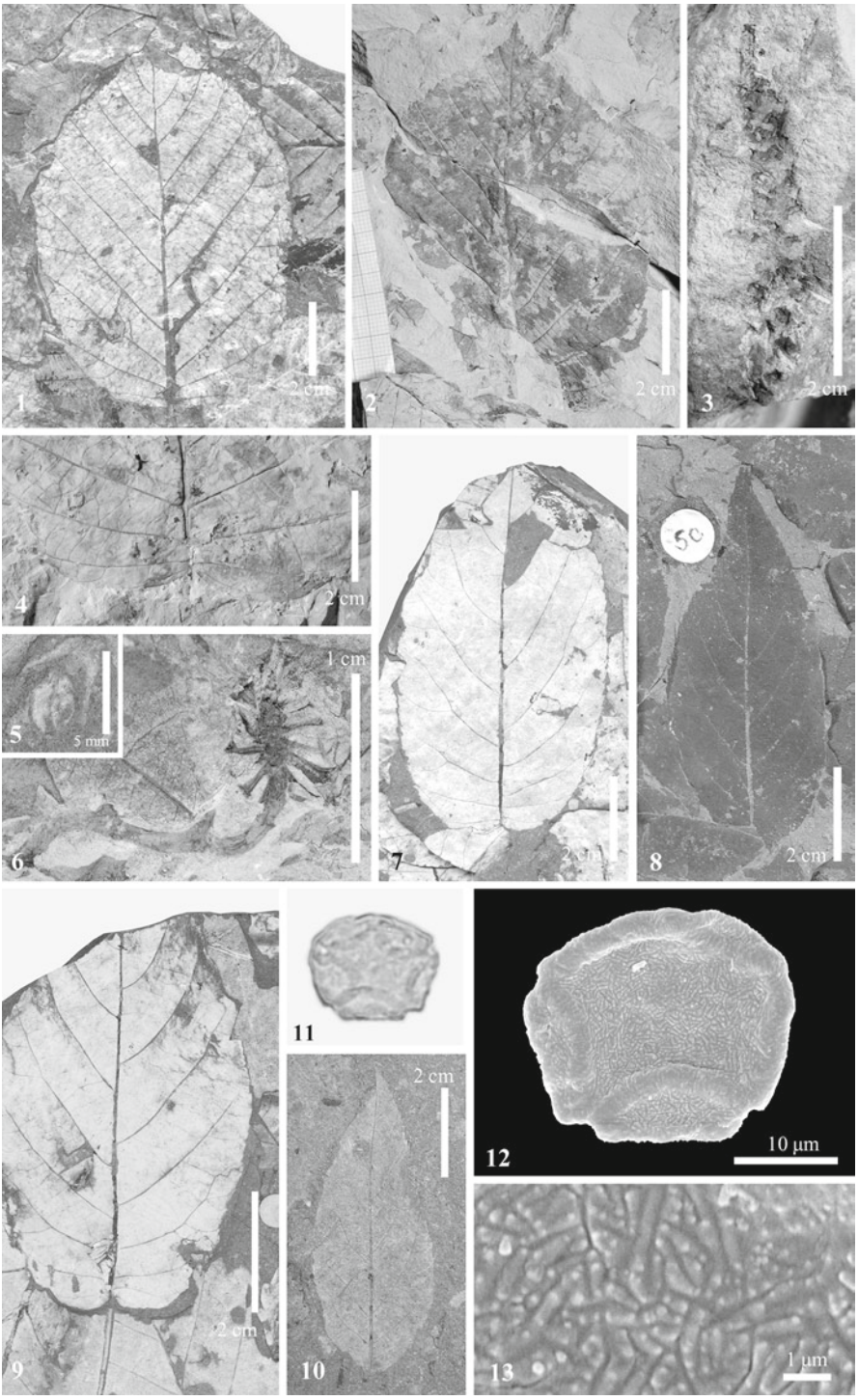

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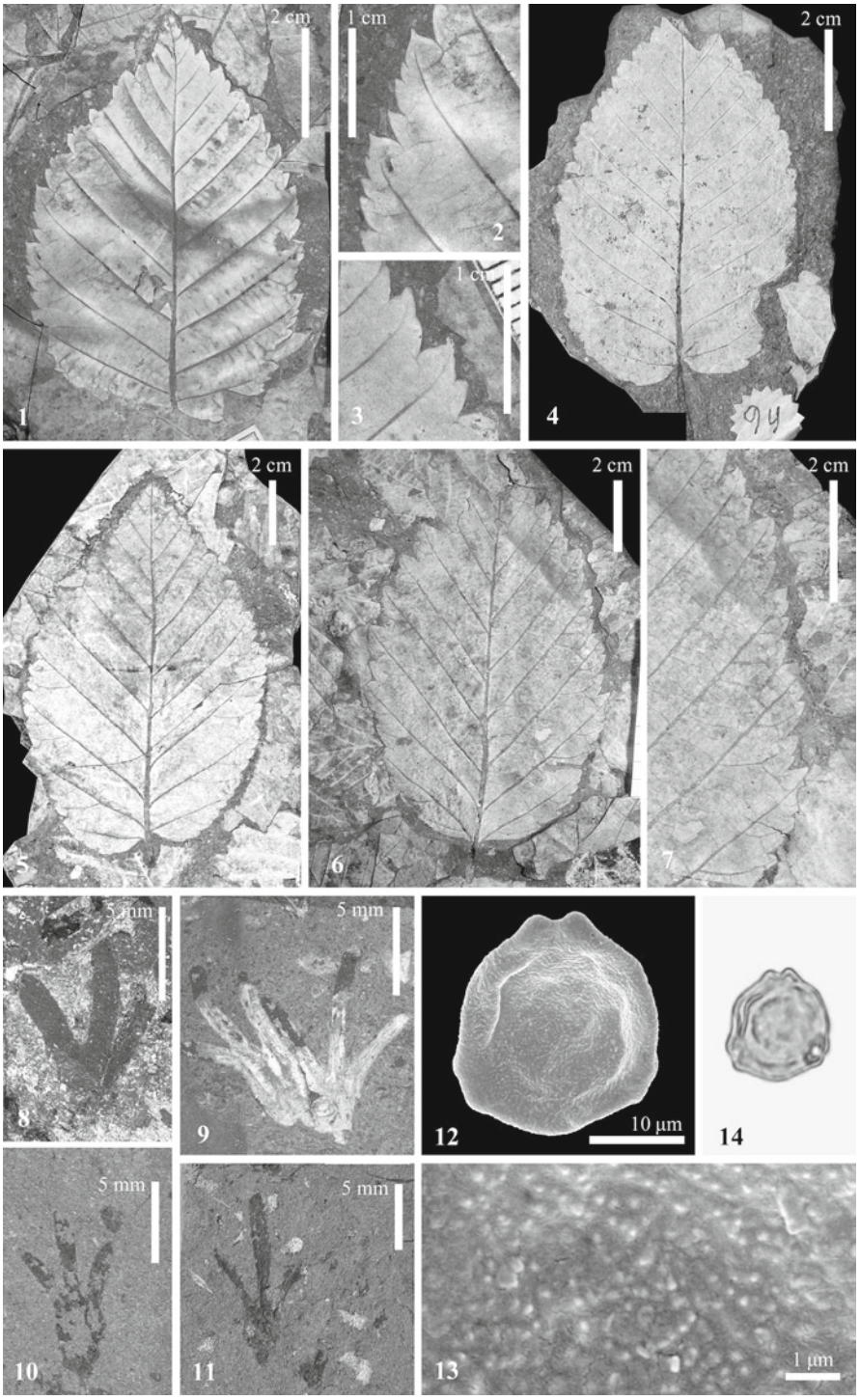

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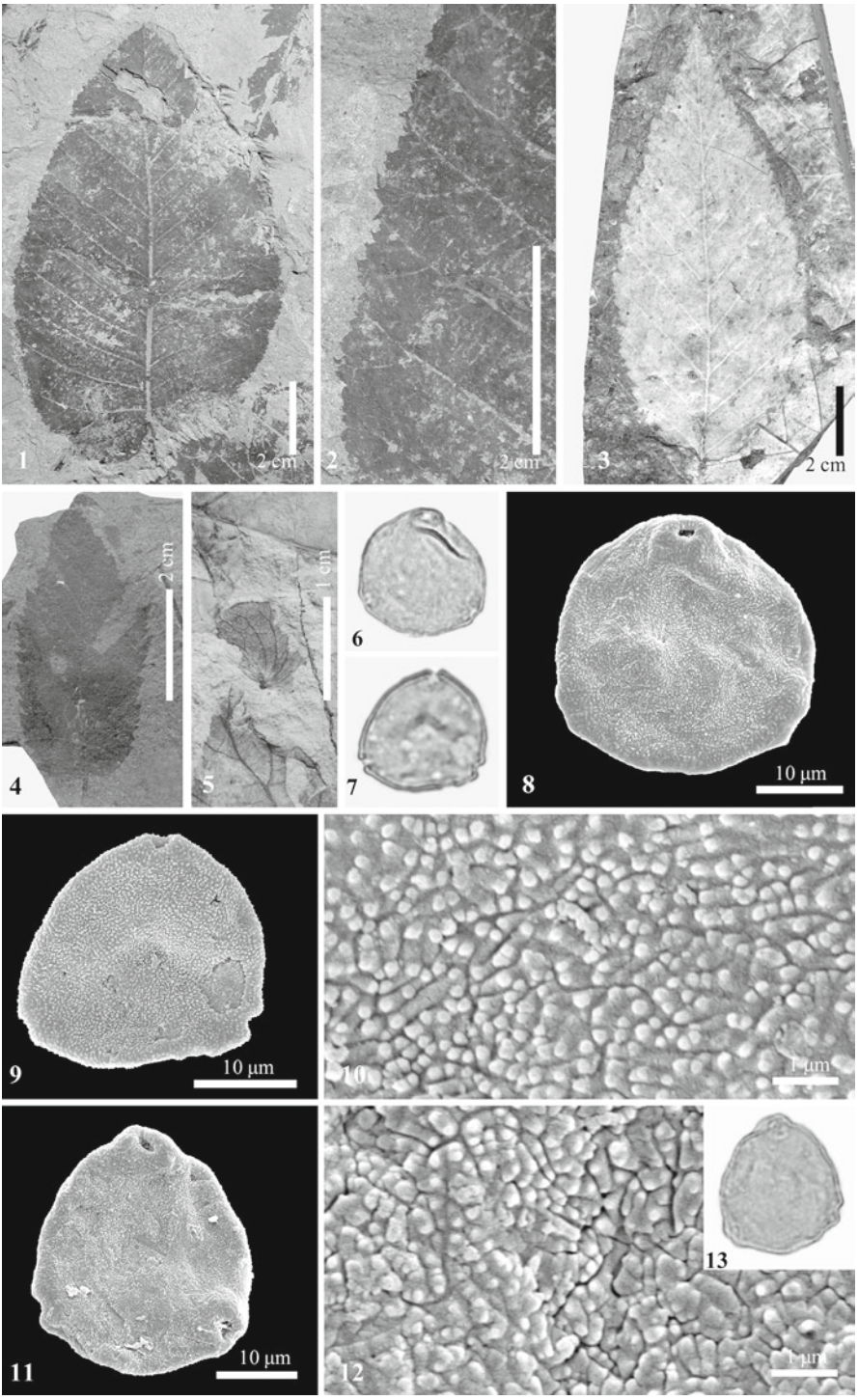

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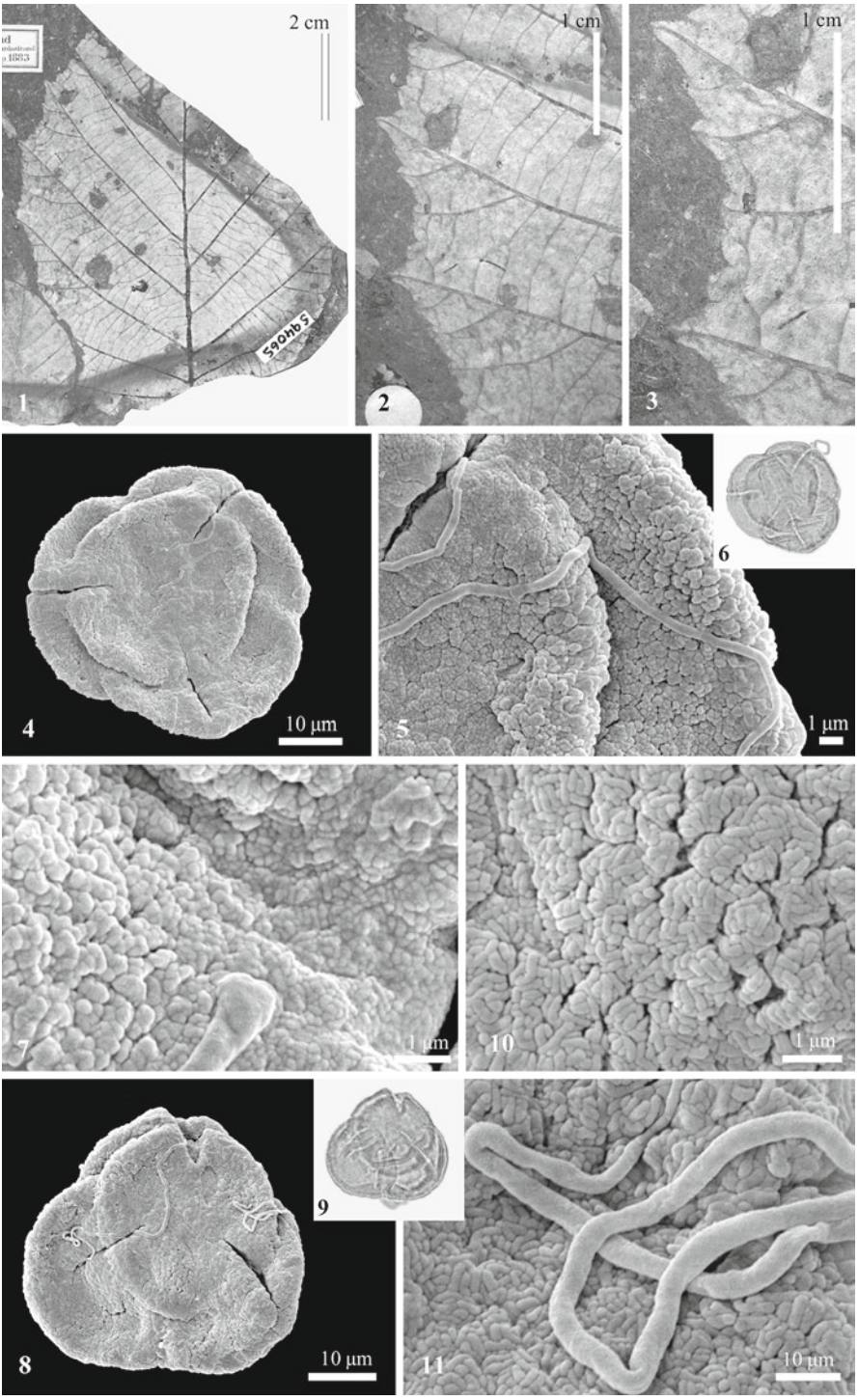



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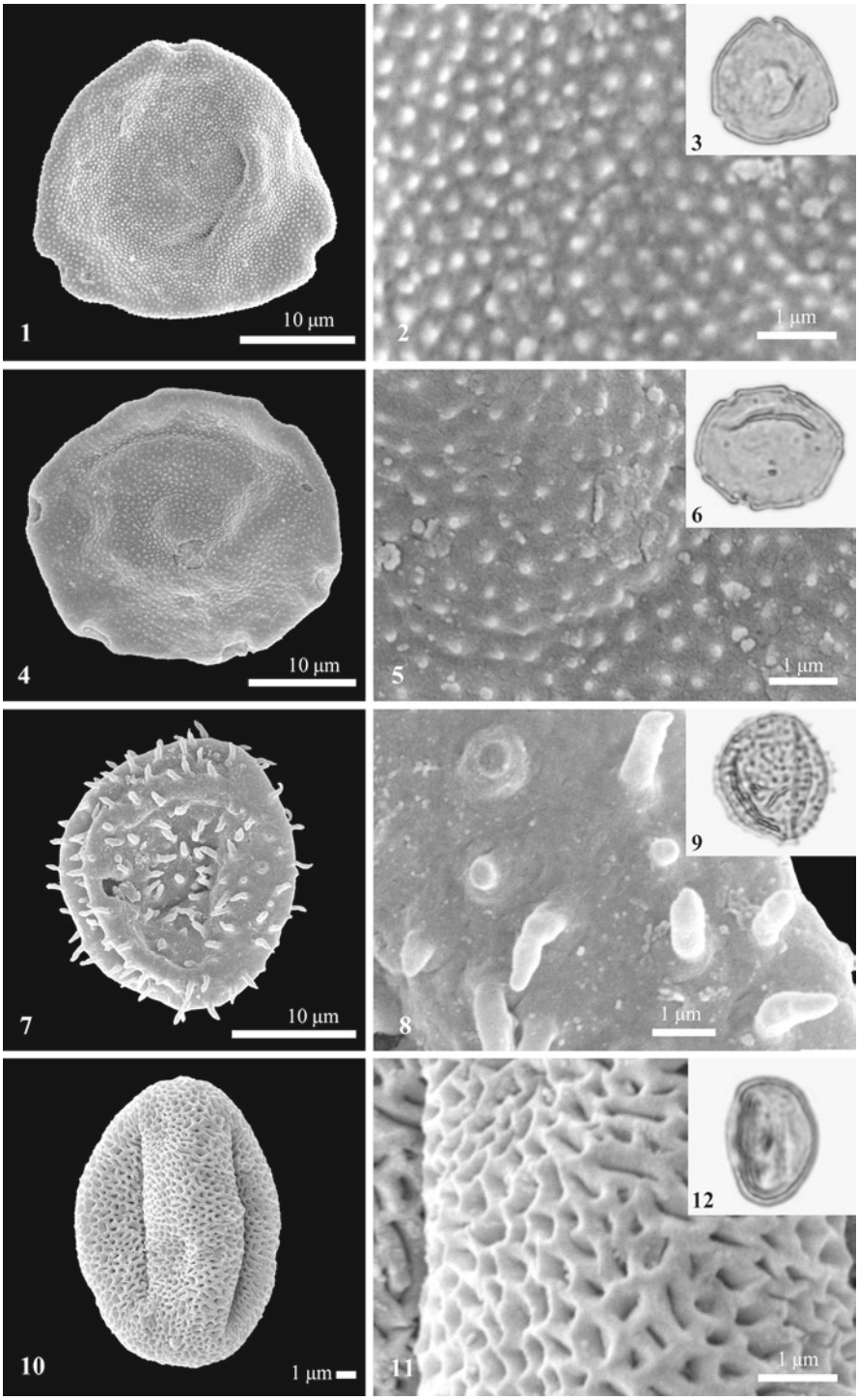



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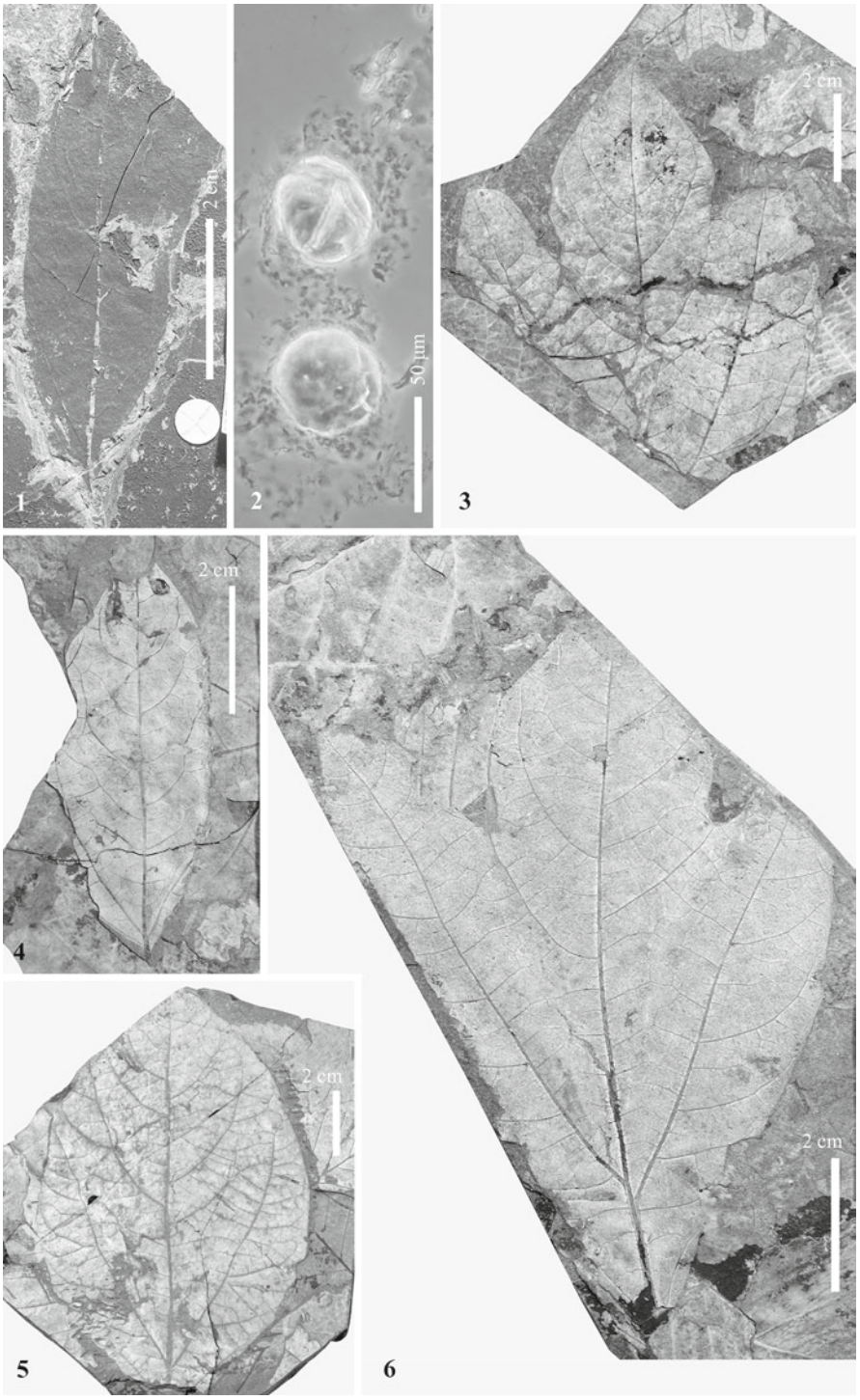



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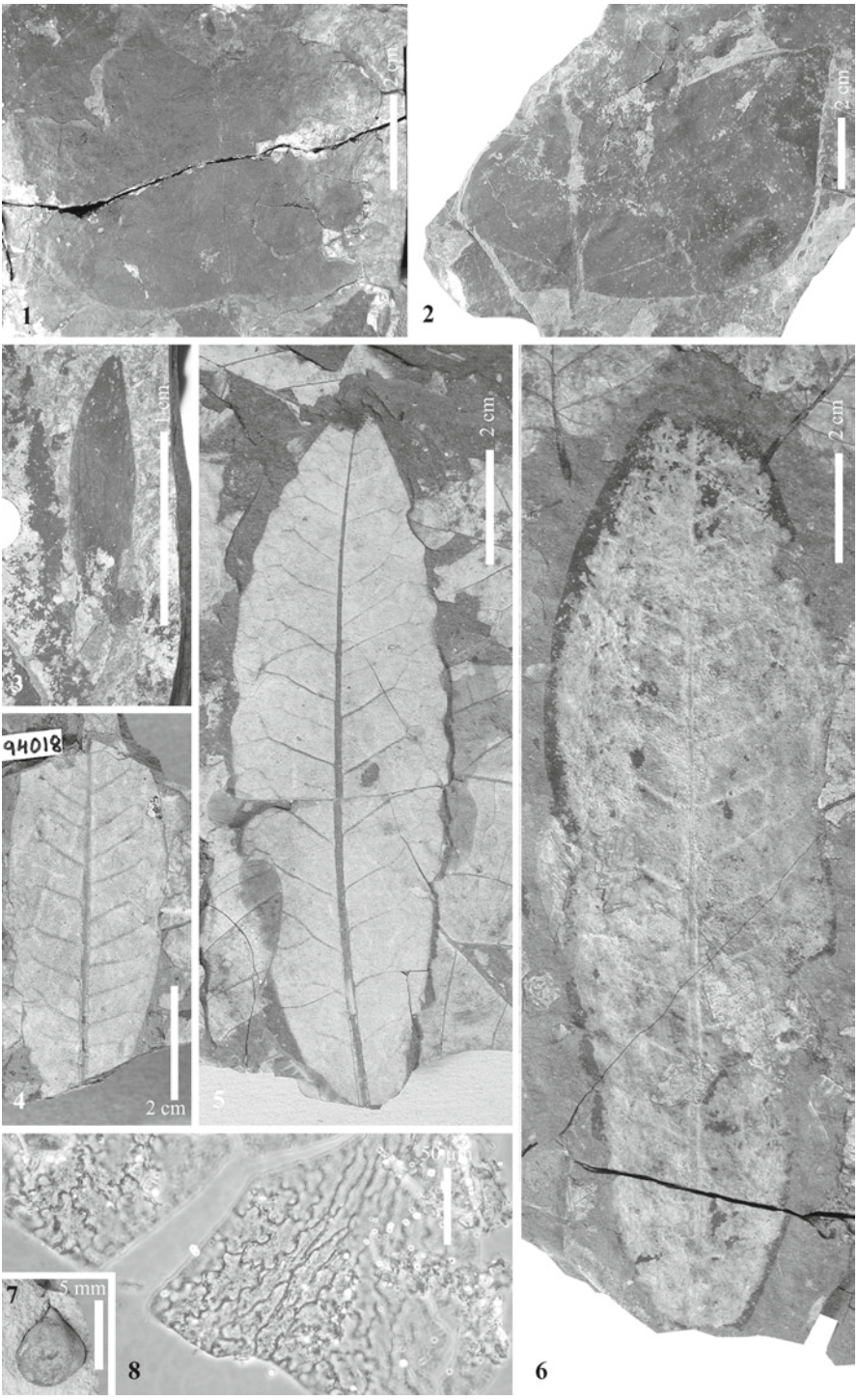



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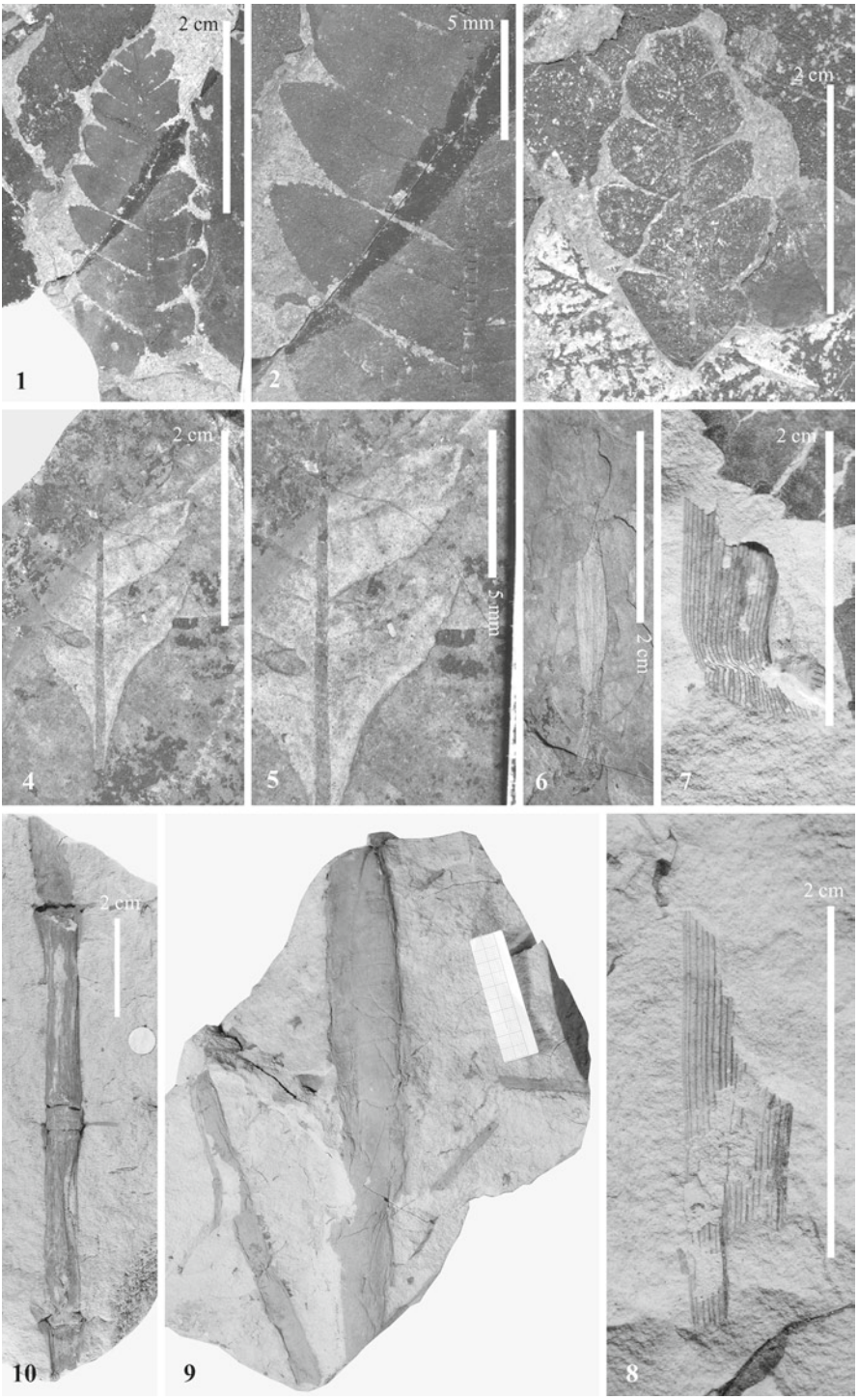



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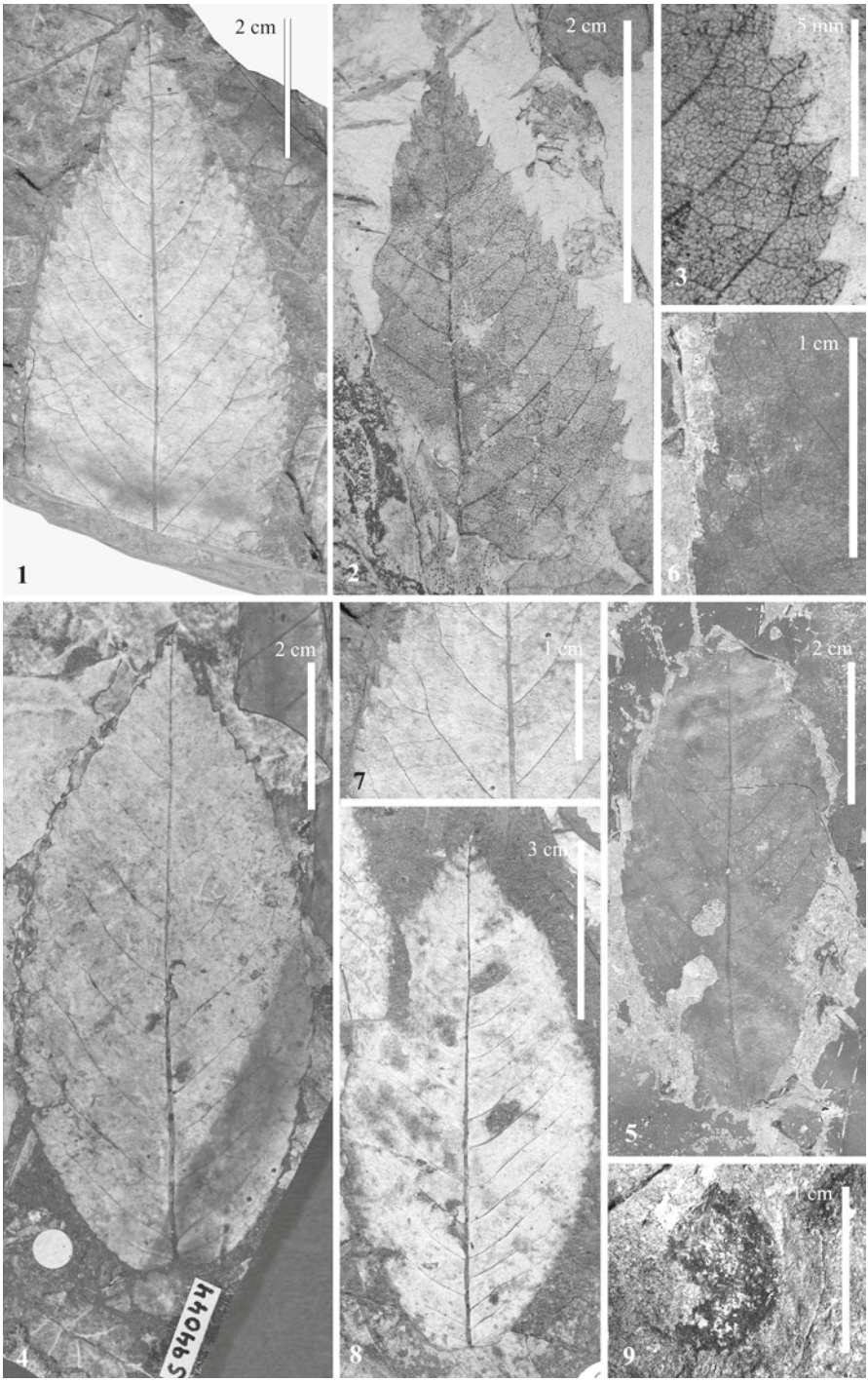



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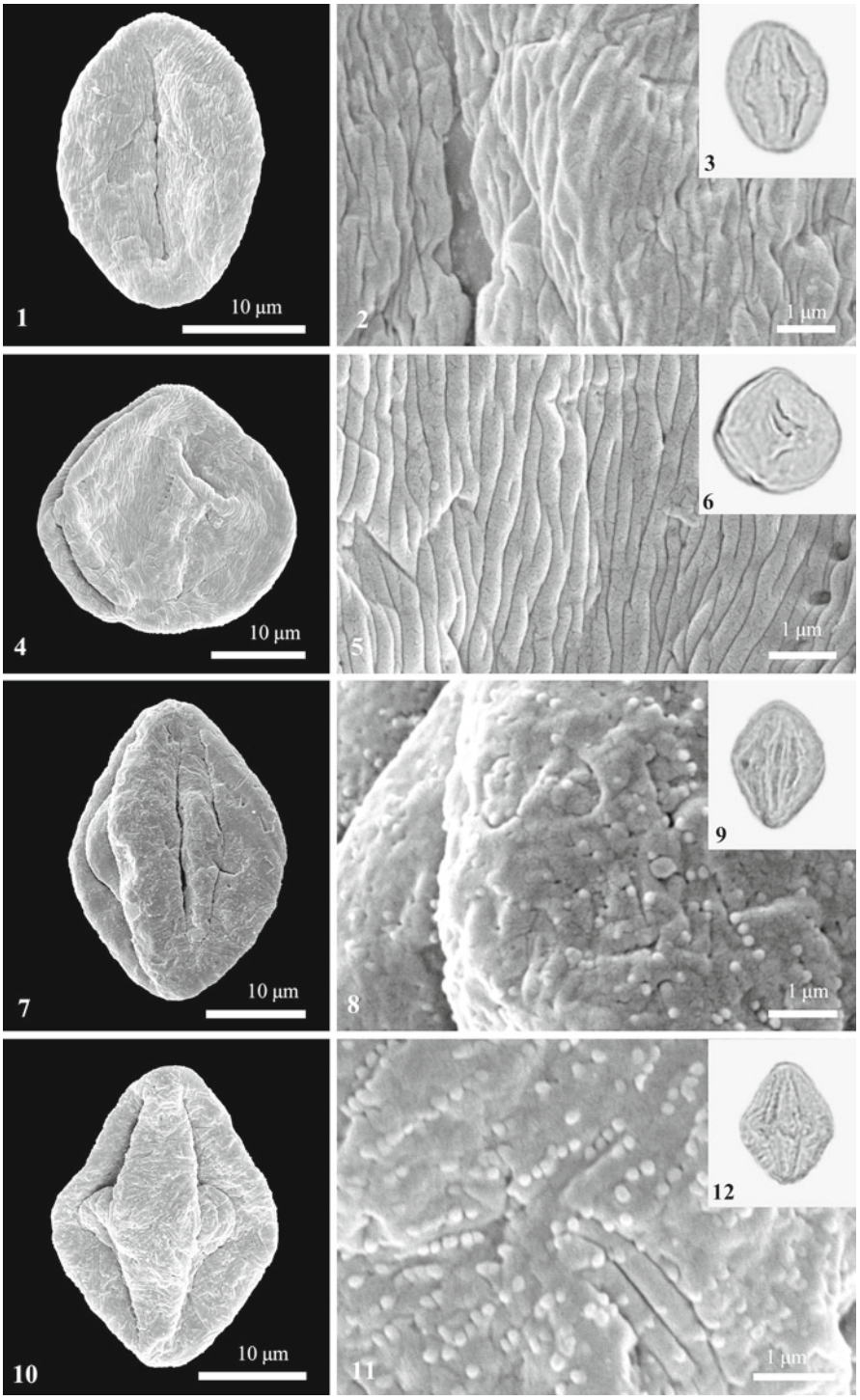



**Plate 5.18**

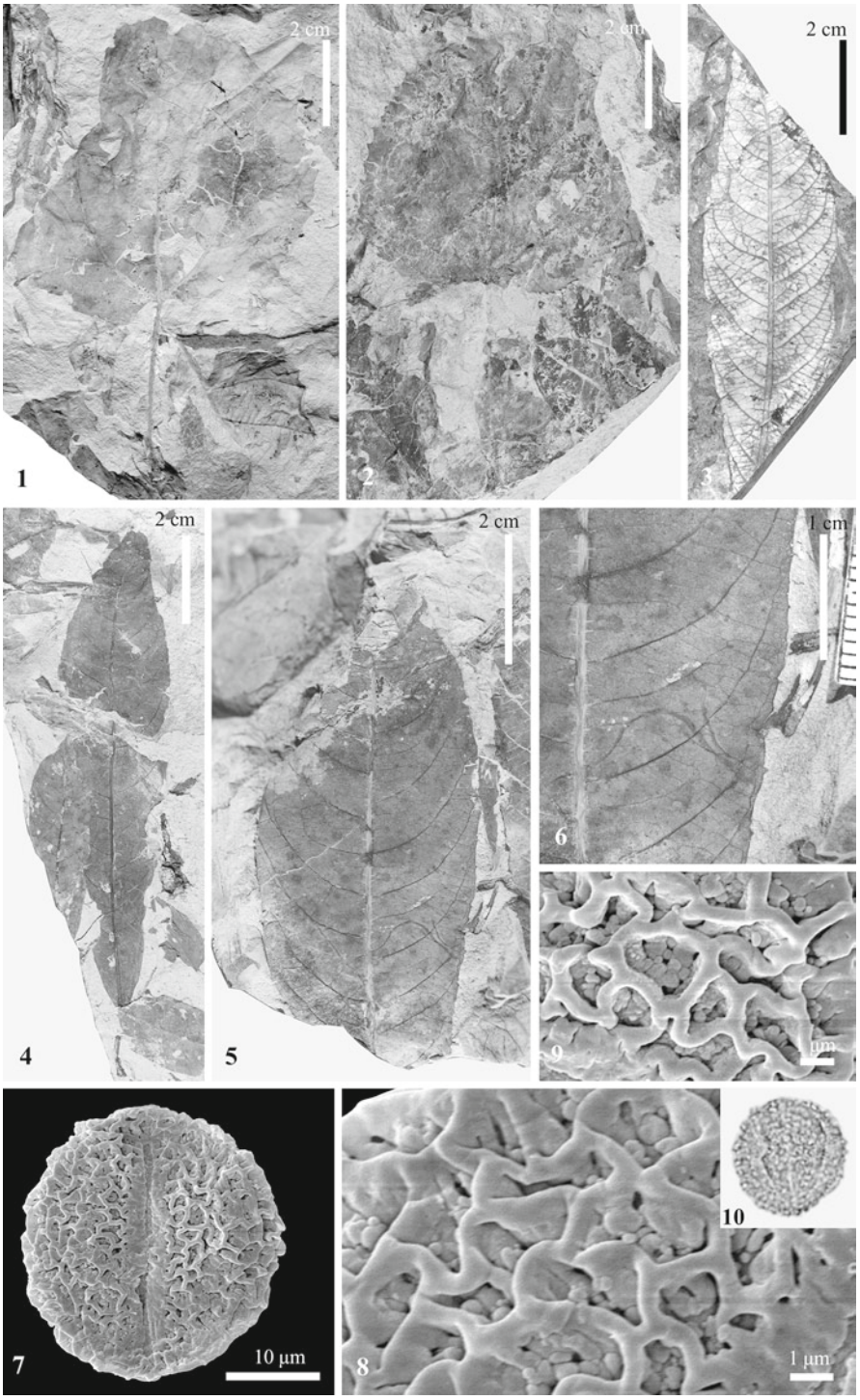



**Plate 5.19**

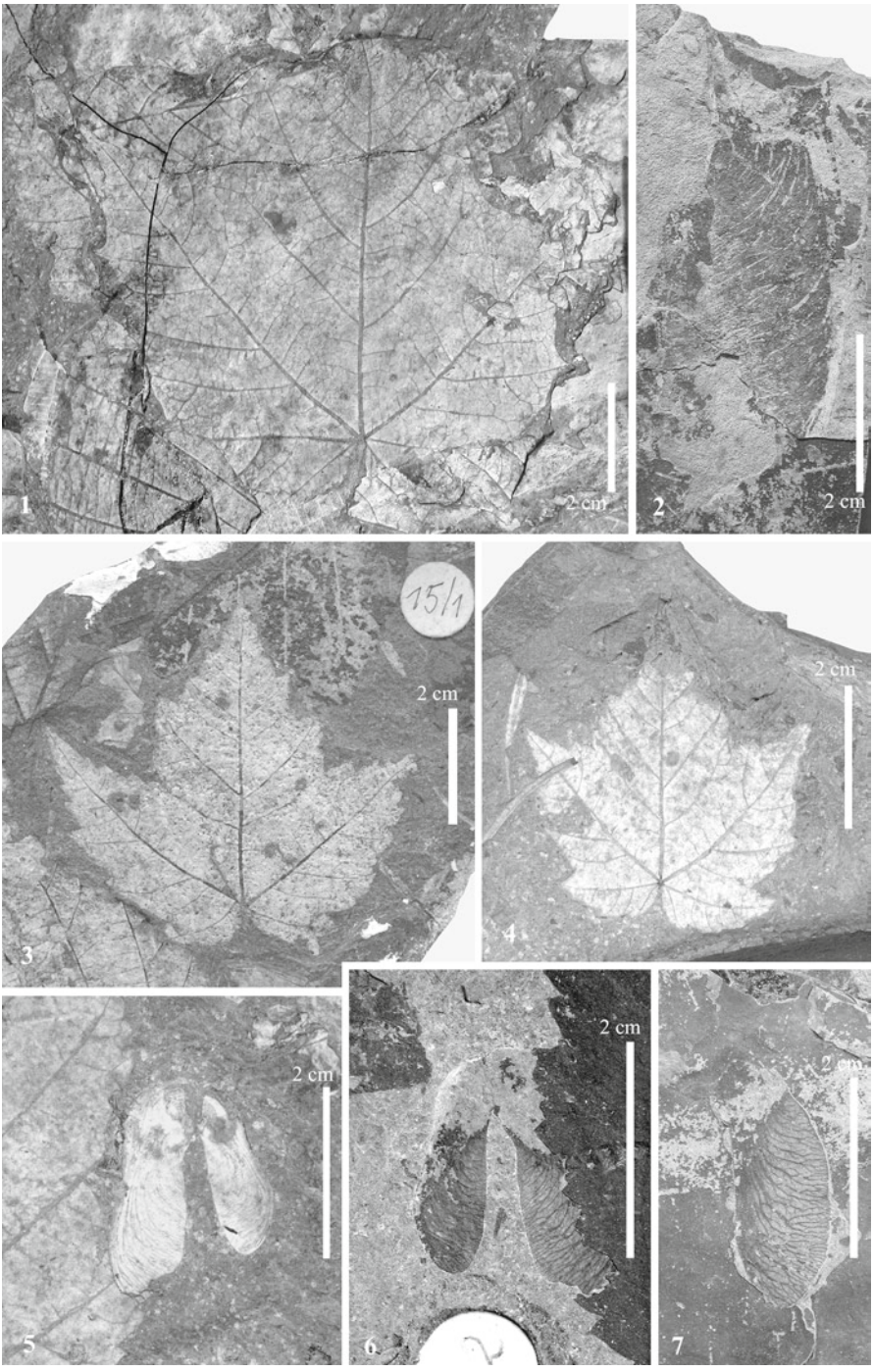



**Plate 5.20**

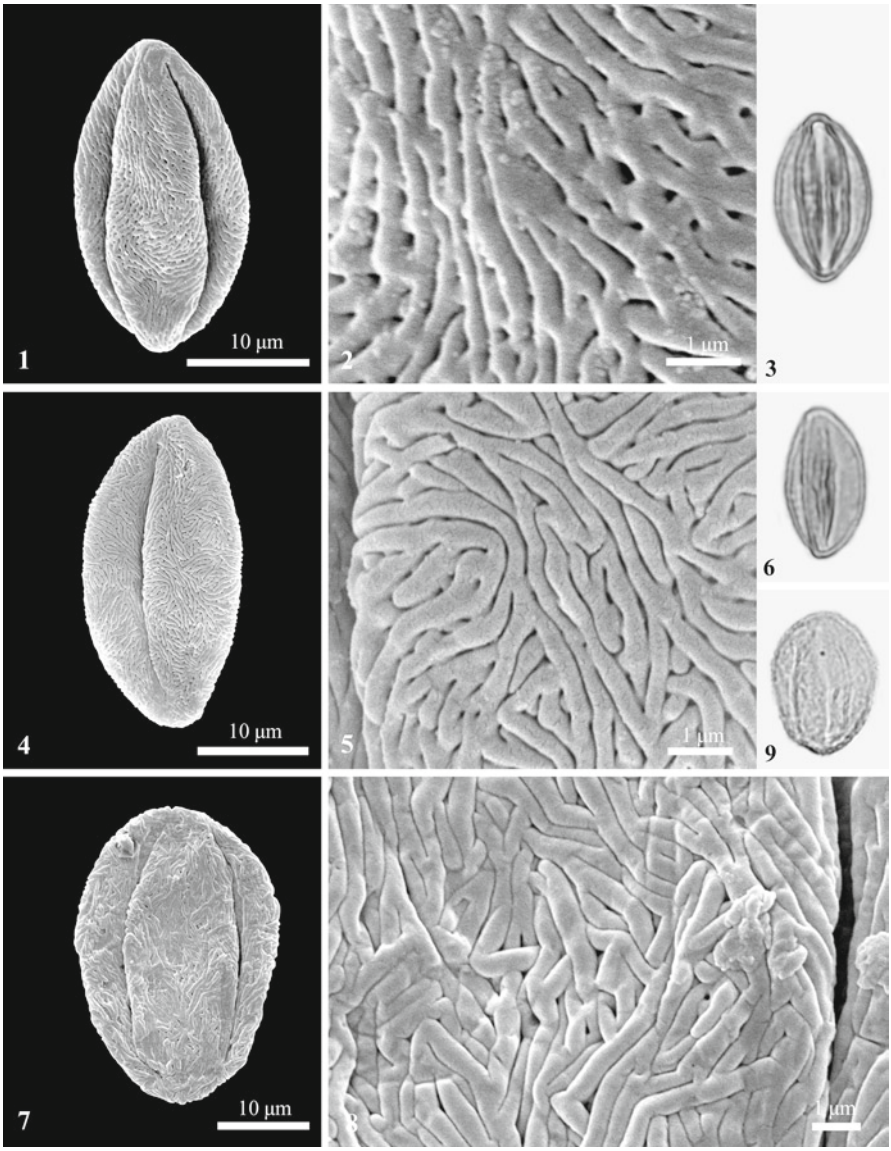



**Plate 5.21**

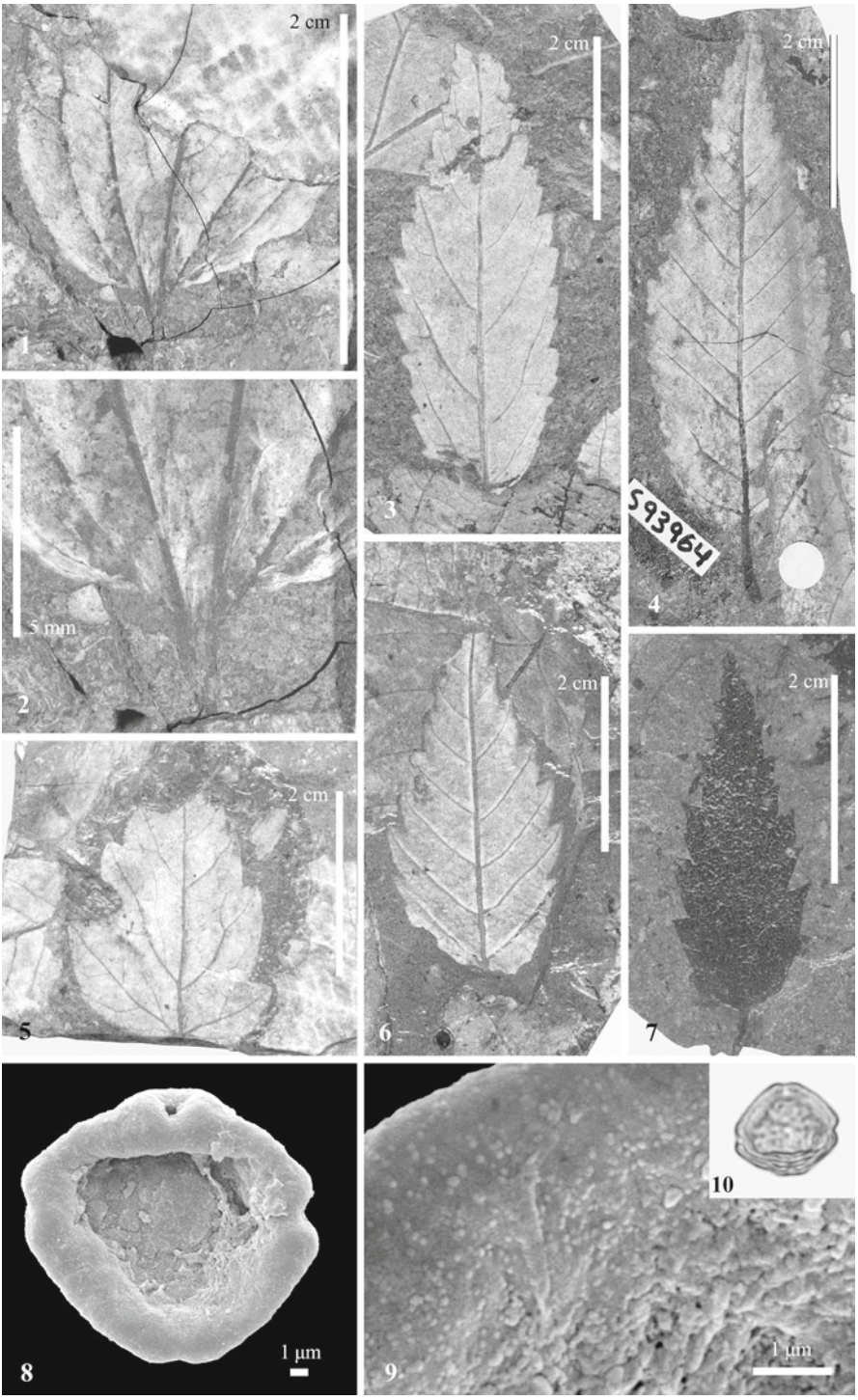



**Plate 5.22**

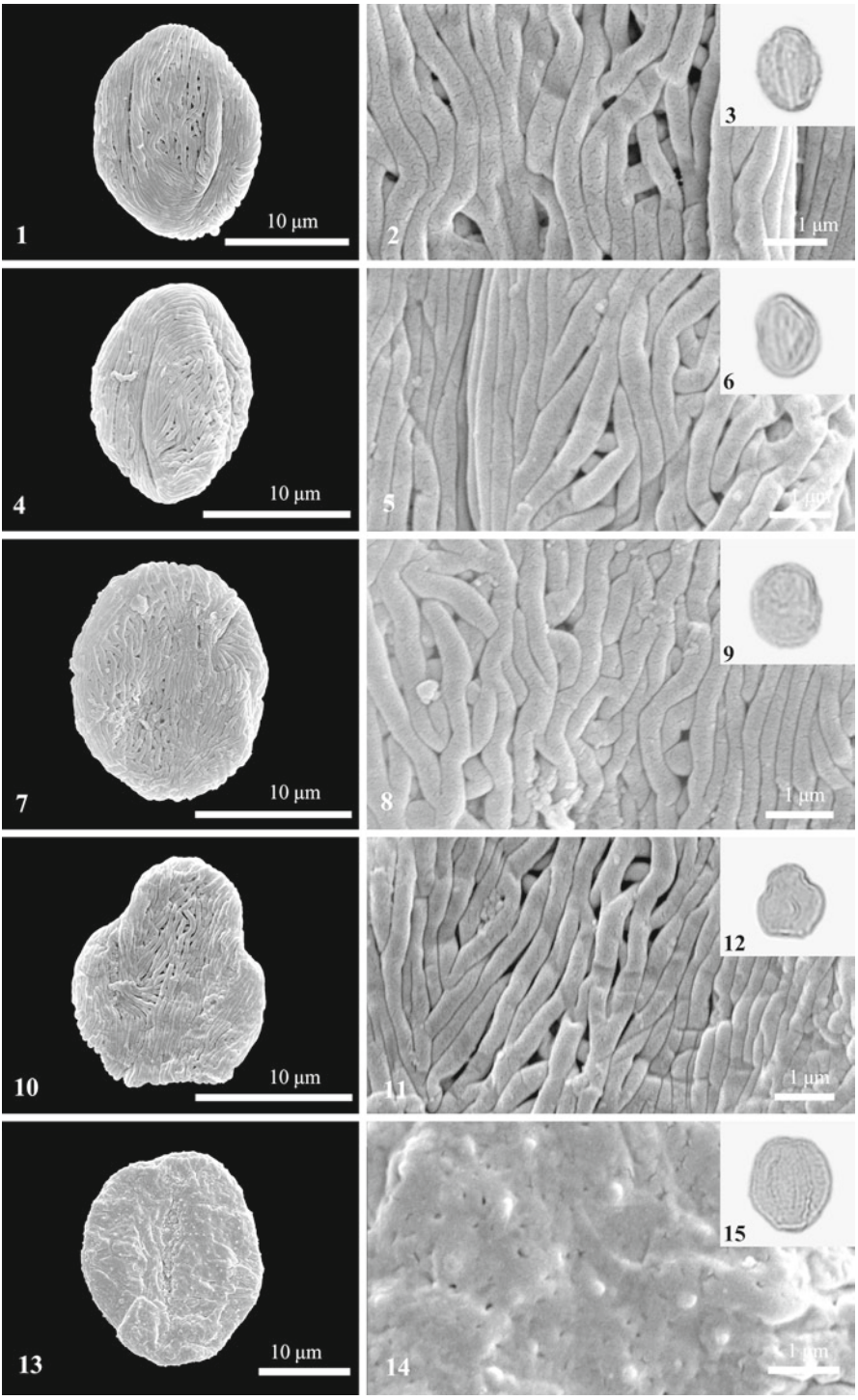

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**Plate 5.23**

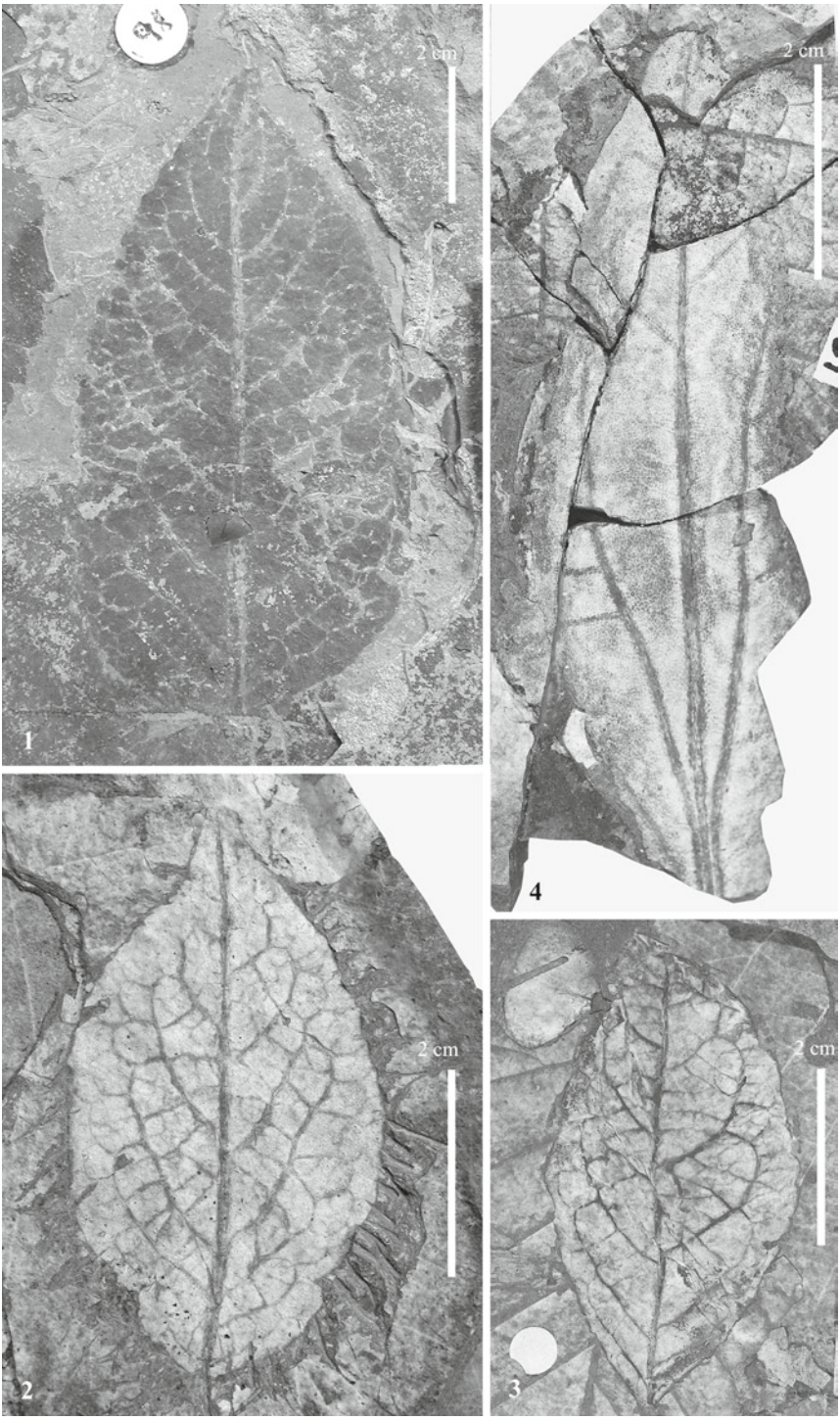



**Plate 5.24**

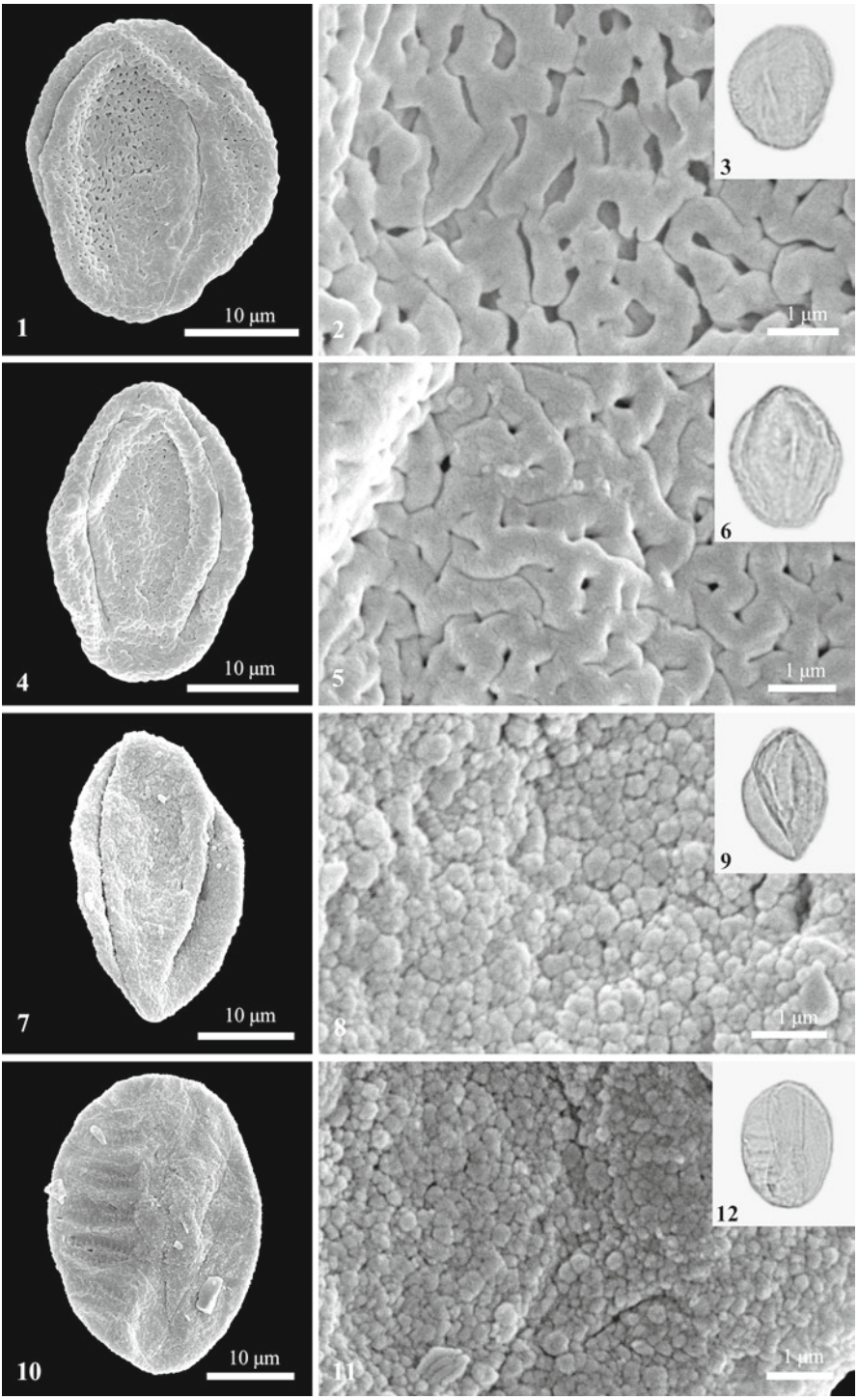



**Plate 5.25**

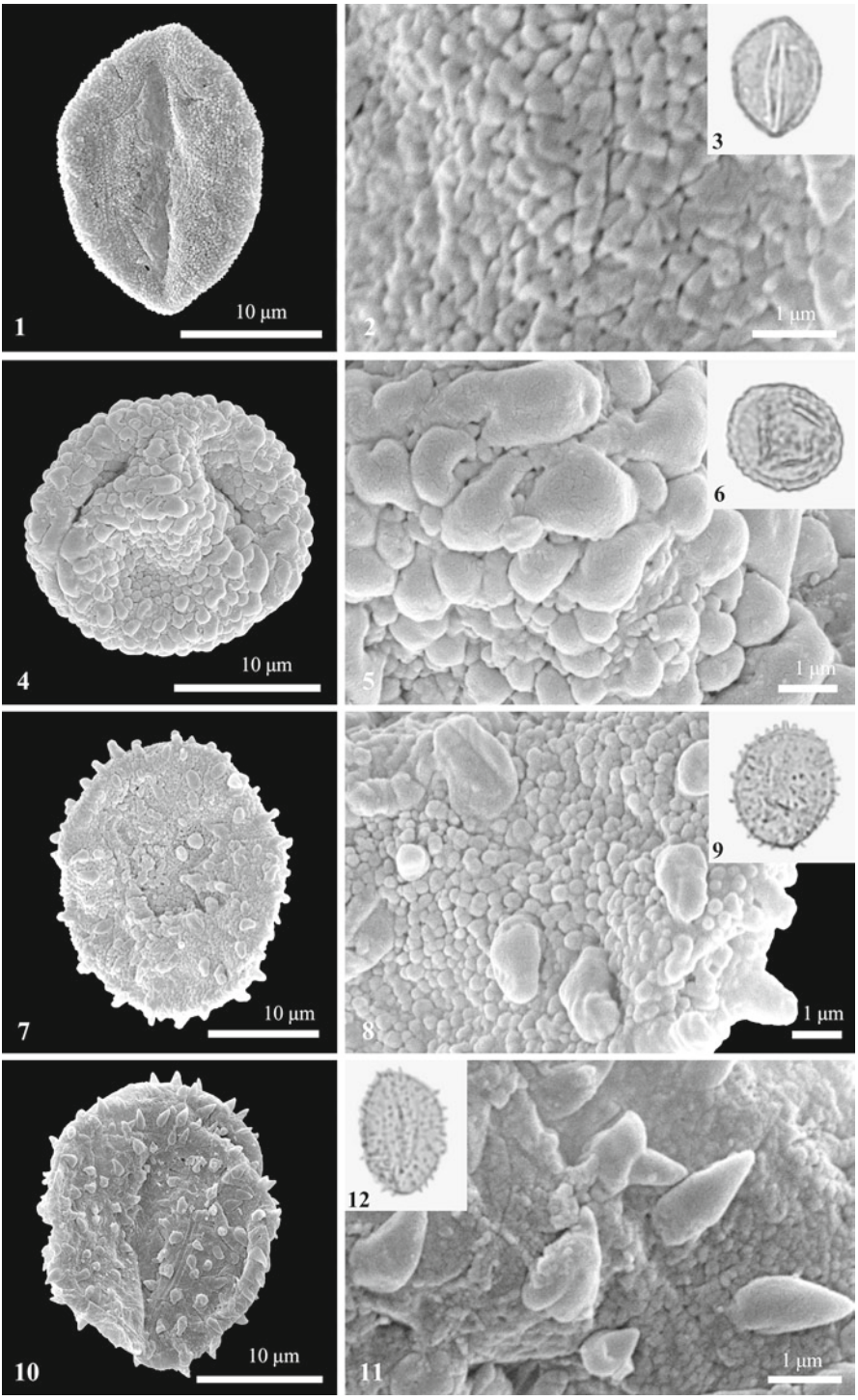



**Plate 5.26**

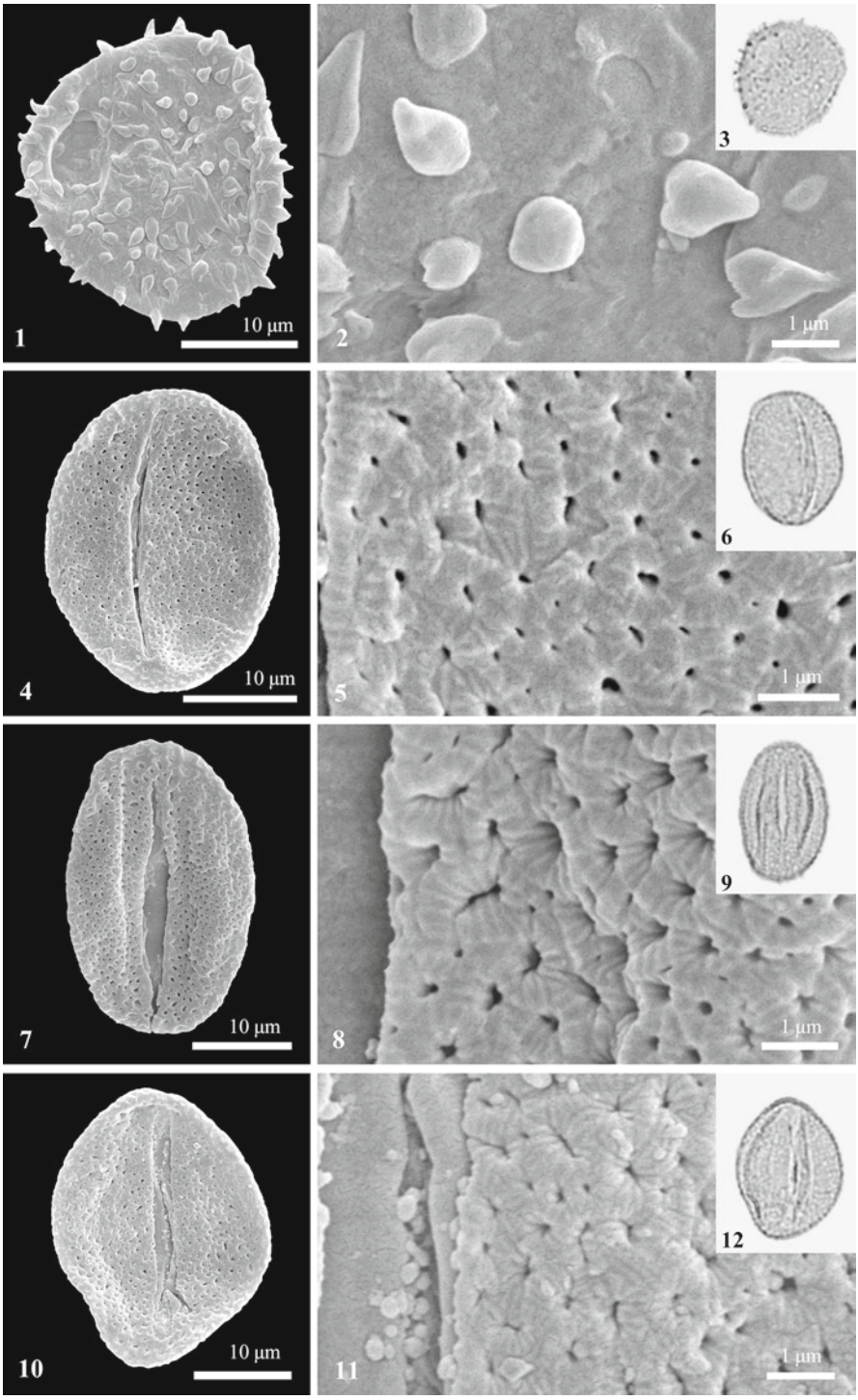



**Plate 5.27**

# Chapter 6
# The Early Late Miocene Floras – First Evidence of Cool Temperate and Herbaceous Taxa

**Abstract** A remarkable change is noticed in the 10 Ma floras of Iceland. In contrast to older floras, herbaceous elements become prominent in the palynological record, and, for the first time, small-leaved Ericaceae are encountered in the macrofossil record. The high number of pollen taxa recovered from sedimentary rock samples of the Tröllatunga-Gautshamar Formation account for the remarkable richness of this flora (ca 100 taxa). Pollen, spores, and macrofossils are all exquisitely preserved. Importantly, many taxa that were characteristic of the older Brjánslækur-Seljá Formation, 12 Ma, have not been recorded from any locality belonging to the 10 Ma and younger formations. Examples for such taxa are: *Glyptostrobus*, *Cryptomeria*, *Sequoia* (Cuppressaceae s. l.), and among the angiosperms *Comptonia*, *Liriodendron*, *Magnolia*, and *Sassafras*. At the same time, a number of warmth-loving taxa occur for the first time in the 10 Ma formation. Most spectacular among the new elements are *Ginkgo* and the extinct Fagaceae *Trigonobalanopsis*, both of which are documented by their pollen. *Pseudotsuga* and *Decodon* are other taxa that appear for the first time in Iceland. In this chapter, the taxonomic composition of the 10 Ma floras of Iceland has been investigated. In addition, floristic turnovers between 12 and 10 Ma, such as the massive appearance of herbaceous taxa, will be discussed in the context of northern hemisphere cooling and continuing land bridge accessibility during the late Middle and early Late Miocene of Iceland.

## 6.1 Introduction

Early Late Miocene plant-bearing sedimentary rocks in Iceland belong to the Tröllatunga-Gautshamar Formation, and are approximately 10 Ma (Tortonian, early Late Miocene; McDougall et al. 1984). The sedimentary rocks, and particularly the frequently appearing lignites and associated plant fossils, have been known for more than 200 years. They were first studied by O. Olavius in 1775–1777 (Olavius 1780). Later, the sediments and lignites of the Tröllatunga-Gautshamar Formation were studied mainly by geologists (Winkler 1863; Thoroddsen 1896, 1906, 1914, 1915; Bárðarson 1918) and in the course of these

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studies, findings of plant fossils from numerous localities were reported. Among these localities are Margrétarfell, Gautshamar, Belti, Torffell, Stekkjargil, Winklerfoss, Gunnustaðagróf, Nónöxl, Bæjarfell, Húsavíkurkleif, Húsavíkurhlíð, Hleypilækur, Fætlingagil, Grýlufoss, Dettifoss, Merkjagil, Hjálparholt, Bæjarlækur, and Nónlækur (see partly Fig. 6.1b, c). Some of the macrofossils were first described by Heer (1859, 1868; collected by J. Steenstrup in 1838–1839, and G. G. Winkler in 1857) and Windisch (1886; collected by C. W. Schmidt and K. Keilhack in 1883) soon after the formation had become better known following Winkler's publication in 1863, mentioning plant fossils from this area. It was much later that other palaeontologists started to work on fossils from the Tröllatunga-Gautshamar Formation. In the early twentieth century, Bárðarson (1931) reported maple leaves from this formation, but most investigations of the plant-bearing sediments were undertaken during the second half of that century. Pflug (1956), Manum (1962), and Akhmetiev et al. (1978) studied the pollen flora of this formation; Friedrich (1968), Símonarson et al. (1975), Akhmetiev et al. (1978), Friedrich and Símonarson (1982), Blokhina (1992), and Símonarson (1991) published on some macrofossil taxa and preservation forms.

Previous studies on pollen from this formation used light microscopy only (Pflug 1956; Manum 1962; Akhmetiev et al. 1978), and accounts dealing with macrofossils have only reported on a single or few taxa (for example Friedrich and Símonarson 1982; Blokhina 1992). Recently, Denk et al. (2005), investigated larger parts of these floras based on macrofossils collected among others by G. Flink in the course of the Swedish Greenland Expedition in 1883, which had not been described earlier. For the present chapter, a combined LM and SEM palynological investigation and a detailed evaluation of macrofossils from all known outcrops of this formation were undertaken. Based on this, we describe palaeoenvironments, vegetation types, and ecological and climatic parameters of possible modern analogues. In addition, we compare the floras of the Tröllatunga-Gautshamar Formation with floras of the older formations in Iceland and with coeval northern hemispheric fossil assemblages and discuss floristic and climatic trends seen within the compared floras.

## 6.2 Geological Setting and Taphonomy

The Tröllatunga-Gautshamar Formation (10 Ma; McDougall et al. 1984) is exposed in the southeastern part of the Northwest peninsula (Fig. 6.1a, b). Sedimentary rocks can be accessed at several outcrops (Margrétarfell, Gautshamar, Belti, Torffell, Stekkjargil, Winklerfoss, Gunnustaðagróf, Nónöxl, Bæjarfell) north of Steingrímsfjörður on the small peninsula bounded by Bjarnarfjörður to the north and Steingrímsfjörður to the south (Fig. 6.1b). Sedimentary rocks are also exposed in Steingrímsfjörður, Húsavíkurkleif locality (Fig. 6.1c; Plate 6.1, 1 and 3) and across the southern part of the Northwest Peninsula, passing the

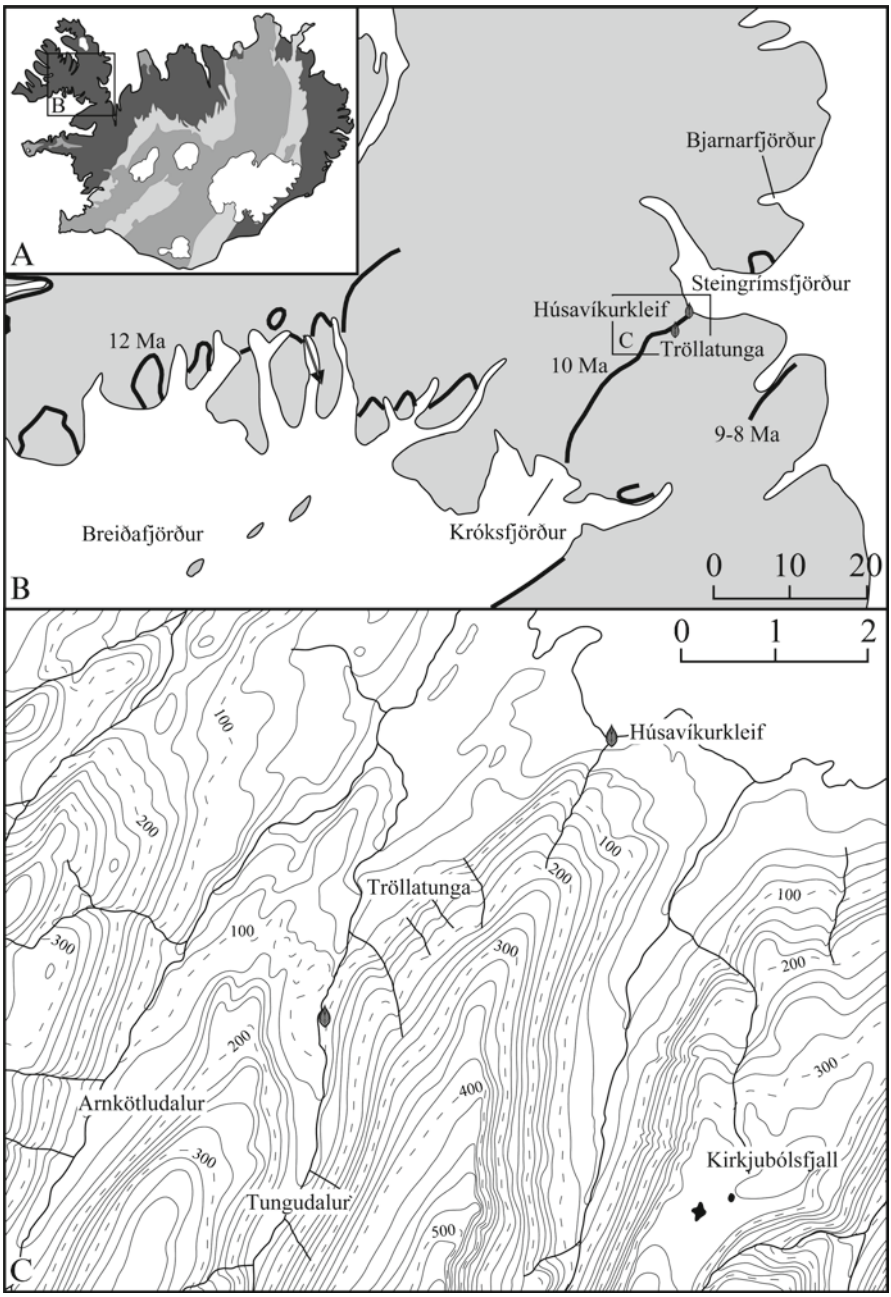



**Fig. 6.1** Map showing fossiliferous localities of the 10 Ma formation. (**a**) bedrock geology (see Fig. 1.10 for explanation), (**b**) extension of sedimentary rock formation, (**c**) Húsavíkurkleif and Tröllatunga localities (Geological background modified after Jóhannesson and Sæmundsson 1989; altitudinal lines from Landmælingar Íslands 1994)

Tröllatunga localities (including the Hleypilækur, Fætlingagil, Grýlufoss, Dettifoss, Merkjagil, Hjálparholt, Bæjarlækur, and Nónlækur outcrops), over to Króksfjörður (Fig. 6.1b).

The sedimentary rocks north of Steingrímsfjörður are fairly similar. They are 7–11 m thick, for the most part composed of brownish to red coloured siltstones and sandstones with occasional tephra layers. The rocks are often organic-rich, showing a more darkish colour with associated lignites. Relatively thick brownish hyaloclastic deposits are often present. One characteristic of this part of the formation is that most of the identifiable plant fossils are preserved as impressions in iron-rich concretions [Iron (II) carbonate ($FeCO_3$)], weathered out from the siltstone units surrounding the lignites. These sedimentary rock types and the typical concretions are the same as found in Húsavíkurkleif south of Steingrímsfjörður (see Plate 6.1, 5 and 7). The sedimentary rocks, especially lignites and organic-rich silt- and sandstone suggest accumulation in a lowland environment, characterized by lakes, rivers and floodplains. The thick hyaloclastic units indicate volcanic eruptions in lakes or areas with high groundwater levels.

The sedimentary rocks in Húsavíkurkleif are covered by 3–5 m thick lava, built up by a series of thin flows from a single eruption. On top of this lava, the Tröllatunga sediments, 5–30 m thick, can be traced all the way from Húsavíkurkleif, to the southwest, up the Tungudalur valley (Fig. 6.1b, c), and over the highlands toward Króksfjörður. The outcrops here are characterized by thick pyroclastic white to yellow pumice-rich rocks (Plate 6.1, 4 and 6) with increasing thickness towards the highlands. They are thought to have originated from the Króksfjarðar central volcano that was active approximately 10 Ma ago. In this part of the formation, plant fossils are found as compressions in white pyroclastic rocks. The best preserved macrofossils are found in very fine-grained tuff units, reworked in lacustrine settings. Most prominent are sediments related to volcanic activity, of which most are more or less *in situ*, while some are reworked or deposited in shallow lacustrine settings. Lignites are not characteristic for this part of the formation, but large stems of trees are often found coalified or petrified in the sediments or even vertically standing and connected to palaeosoil, and penetrating the volcanic sediments and/or overlying lavas.

## 6.3 Floras, Vegetation, and Palaeoenvironments

A total of 99 taxa were recognized from the Tröllatunga-Gautshamar Formation (Table 6.1, Plates 6.1–6.47). One third belongs to the woody angiosperms (34 taxa) and another third to the herbaceous angiosperms (31 taxa). Conifers (incl. *Ginkgo*) comprise eight taxa and bryophytes and pteridophytes 11 taxa. Lianas are few (only two taxa) and the remaining taxa are unknown types (Fig. 6.2). There is a substantial difference between the number of taxa represented by pollen and macrofossils (90 versus 22).

Macrofloras from the Húsavíkurkleif outcrop and other localities north of Steingrímssfjörður are composed of a few taxa only, mostly fragments of

**Table 6.1** Taxa recorded for the 10 Ma floras of Iceland

| Tröllatunga-Gautshamar Formation<br>Taxa | Pollen | Leaves | RP | Other | DM |
|---|---|---|---|---|---|
| Bryophyta | | | | | |
| *Sphagnum* sp. | + | | | | 1a |
| Lycopodiaceae | | | | | |
| *Lycopodium* sp. | + | | | | 1a |
| *Huperzia* sp. | + | | | | 1a |
| Osmundaceae | | | | | |
| *Osmunda parschlugiana* | + | **+** | | | 1a |
| Polypodiopsida | | | | | |
| Pteridophyta gen. et spec. indet. 1 | | + | | | 1a |
| Equisetaceae | | | | | |
| *Equisetum* sp. | | + | | + | 1a |
| Polypodiaceae | | | | | |
| *Polypodium* sp. 1 | + | | | | 1a |
| Polypodiaceae gen. et spec. indet. 1 | + | | | | 1a |
| Polypodiaceae gen. et spec. indet. 3 | + | | | | 1a |
| Polypodiaceae gen. et spec. indet. 4 | + | | | | 1a |
| Polypodiaceae gen. et spec. indet. 5 | + | | | | 1a |
| Ginkgoaceae | | | | | |
| *Ginkgo* sp. | + | | | | 1b |
| Pinaceae | | | | | |
| *Abies* sp. | + | | | | |
| *Larix* sp. | (+) | | | + | 2a |
| *Picea* sect. *Picea* | + | | + | | 2a |
| *Pinus* sp. 1 (Diploxylon type) | + | | | | 2a |
| *Pseudotsuga* sp. | (+) | | + | | 2a |
| *Tsuga* sp. 1 | + | | | | 2a |
| Sciadopityaceae | | | | | |
| *Sciadopitys* sp. | + | | | | 2a |
| Apiaceae | | | | | |
| Apiaceae gen. et spec. indet. 1 | + | | | | 1b |
| Apiaceae gen. et spec. indet. 2 | + | | | | 1b |
| Apiaceae gen. et spec. indet. 3 | + | | | | 1b |
| Apiaceae gen. et spec. indet. 4 | + | | | | 1b |
| Asteraceae | | | | | |
| *Artemisia* sp. 1 | + | | | | 1a |
| *Artemisia* sp. 2 | + | | | | 1a |
| Asteraceae gen. et spec. indet. 1 | + | | | | 1a |
| Asteraceae gen. et spec. indet. 2 | + | | | | 1a |
| Asteraceae gen. et spec. indet. 3 | + | | | | 1a |
| Betulaceae | | | | | |
| *Alnus cecropiifolia* | (+) 3 | **+** | (+) D | | 1a, 2a |
| *Betula islandica* | + | **+** | | | 1a |
| *Carpinus* sp. 2 | + | | | | 2a |
| *Corylus* sp. | + | | | | 2a |
| Calycanthaceae | | | | | |
| aff. Calycanthaceae | + | | | | 1b |

(continued)

**Table 6.1** (continued)

| Tröllatunga-Gautshamar Formation<br>Taxa | Pollen | Leaves | RP | Other | DM |
|---|---|---|---|---|---|
| Caprifoliaceae | | | | | |
| *Lonicera* sp. 1 | + | | | | 1b |
| *Lonicera* sp. 2 | + | | | | 1b |
| *Lonicera* sp. 3 | + | | | | 1b |
| Caryophyllaceae | | | | | |
| Caryophyllaceae gen et. spec. indet. 1 | + | | | | 1b |
| Caryophyllaceae gen et. spec. indet. 2 | + | | | | 1b |
| Caryophyllaceae gen et. spec. indet. 3 | + | | | | 1b |
| Chenopodiaceae | | | | | |
| *Chenopodium* sp. | + | | | | 1b |
| Chenopodiaceae gen. et spec. indet. 1 | + | | | | 1b |
| Chenopodiaceae gen. et spec. indet. 2 | + | | | | 1b |
| Cyperaceae | | | | | |
| Cyperaceae gen. et spec. indet. A | | + | | | 1b |
| Ericaceae | | | | | |
| *Arctostaphylos* sp. | | + | | | 1b |
| *Rhododendron* aff. *ponticum* | (+) | **+** | | | 1a?, 2a |
| Ericaceae gen. et spec. indet. 1 | + | | | | 1b |
| *Vaccinium* sp | | **+** | | | 1b |
| Fagaceae | | | | | |
| *Fagus* sp. | + | | | | 2b, 3 |
| *Trigonobalanopsis* sp. | + | | | | 2b, 3 |
| Juglandaceae | | | | | |
| *Cyclocarya* sp. | (+) | + | | | 2a |
| *Pterocarya* sp. | (+) | + | | | 2a |
| Liliaceae | | | | | |
| Liliaceae gen. et spec. indet. 2 | + | | | | 2a |
| Liliaceae gen. et spec. indet. 3 | + | | | | 2a |
| Lythraceae | | | | | |
| *Decodon* sp. | + | | | | 1b |
| Nympheaceae | | | | | |
| cf. *Nuphar* sp. | | + | | | 1b |
| Plantaginaceae | | | | | |
| aff. *Plantago lanceolata* | + | | | | 1b |
| Platanaceae | | | | | |
| *Platanus* sp. | + | | | | 2a |
| Poaceae | | | | | |
| Poaceae gen. et spec. indet. 1 | + | | | | 1b, 2a |
| Polygonaceae | | | | | |
| *Polygonum* sect. *Aconogonon* sp. | + | | | | 1b |
| *Rumex* sp. | + | | | | 1b |
| Ranunculaceae | | | | | |
| *Anemone* sp. | + | | | | 1b, 2a |
| *Ranunculus* sp. 1 | + | | | | 1b |

(continued)

**Table 6.1** (continued)

| Tröllatunga-Gautshamar Formation<br>Taxa | Pollen | Leaves | RP | Other | DM |
|---|---|---|---|---|---|
| *Thalictrum* sp. 1 | + | | | | 1b |
| Ranunculaceae gen. et spec. indet. 1 | + | | | | 1b |
| Ranunculaceae gen. et spec. indet. 2 | + | | | | 1b |
| Rosaceae | | | | | |
| Rosaceae gen. et spec. indet. Type A | (+) 7 | + | | | 1b |
| *Crataegus* sp. | + | | | | |
| *Sanguisorba* sp. | + | | | | 1b, 2a |
| Salicaceae | | | | | |
| *Salix gruberi* | (+) 2 | **+** | | | 1a |
| Sapindaceae | | | | | |
| *Acer crenatifolium* subsp. *islandicum* | (+) 3 | **+** | + D | | 2a |
| *Acer askelssonii* | (+) 3 | + | **+** D | | 2a |
| Smilacaceae | | | | | |
| *Smilax* sp | | + | | | 1b |
| Tiliaceae | | | | | |
| *Tilia* sp. | + | | | | 1b?, 2a |
| Ulmaceae | | | | | |
| *Ulmus* sp. | + | | | | 2a |
| Vitaceae | | | | | |
| *Parthenocissus* sp. | + | | | | 1b |
| Incertae sedis - Magnoliophyta | | | | | |
| *Dicotylophyllum* sp. B | | + | | | ? |
| *Dicotylophyllum* sp. C | | + | | | ? |
| Pollen type 8 | + | | | | ? |
| Pollen type 9 | + | | | | ? |
| Pollen type 10 | + | | | | ? |
| Pollen type 11 | + | | | | ? |
| Pollen type 12 | + | | | | ? |
| Pollen type 13 | + | | | | ? |
| Pollen type 14 | + | | | | ? |
| Pollen type 15 | + | | | | ? |
| Pollen type 16 | + | | | | ? |
| Pollen type 17 | + | | | | ? |
| Pollen type 18 | + | | | | ? |
| Pollen type 19 | + | | | | ? |
| Pollen type 20 | + | | | | ? |

*L* leafy axis, *A* fruit attached to leafy axis, *D* fruit dispersed, *RP* reproductive structure, + organ present, **+** original description of species based on this organ, (+) organ belonging to genus but uncertain to which of the species, (+) 2 indicating number of pollen types possibly belonging to the eponymous morphotaxon, *DM* Dispersal mode: 1a wind long distance (anemochory), 1b bird long distance (endozoochory), 2a wind short distance (anemochory), 2b animals short distance (exozoochory), 3 dyschory

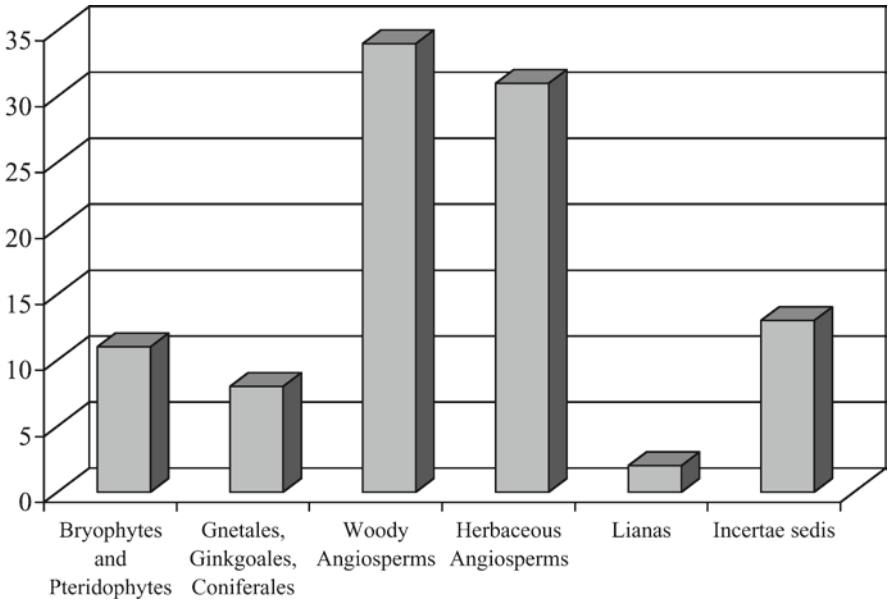



**Fig. 6.2** Distribution of life forms and higher taxa among the plants recovered from the 10 Ma sedimentary rock formation. Height of columns indicates number of taxa

*Osmunda* fronds and axes of *Equisetum* with an admixture of *Salix* leaves and *Alnus* strobili. *Betula*, *Pterocarya*, and *Acer* are less common. Azonal or riparian elements and the type of the sedimentary rocks reflect lowland environments dominated by lakes, rivers, and floodplains. South of Húsavíkurkleif, the macrofloras in the Tröllatunga area are richer and composed mostly of *Acer*, *Alnus*, *Cyclocarya*, *Rhododendron*, Rosaceae, and *Vaccinium*. Other taxa include *Betula*, *Smilax*, *Arctostaphylos*, *Picea*, and *Pseudotsuga*. The diversity and heterogeneity of the fossil flora and the type of sedimentary rocks suggest that these assemblages reflect zonal vegetation, growing on generally drier substrates with a few widely spaced shallow lakes or ponds in an elevated area that was greatly affected by volcanic activity.

Combined macrofossil and palynological evidence allow for a more differentiated reconstruction of the early Late Miocene vegetation types and environments. Nine main vegetation types can be distinguished (Table 6.2, Fig. 6.3). Azonal riparian vegetation is represented by plants characteristic of aquatic and subaquatic environments, and backswamp forests and temporarily flooded lake margins. Temporarily flooded forests were quite diverse, containing trees, shrubs, true lianas, and herbaceous plants in forest gaps. Warmth-loving Cupressaceae as encountered in the older formations (see Chaps. 4 and 5) are entirely absent from the Tröllatunga-Gautshamar Formation and large trees in temporally flooded riparian forests were probably species of *Pterocarya*, *Alnus*, and *Salix*, and possibly also some Rosaceae.

**Table 6.2** Vegetation types and their components during the late early Late Miocene of Iceland

| Vegetation types 10 Ma | | | | | |
|---|---|---|---|---|---|
| **Aquatic vegetation**<br>*Decodon* sp.<br>Lemnaceae gen. et spec. indet. 1<br>cf. *Nuphar* sp.<br>Ranunculaceae gen. et spec. indet. 1, 2 | **Backswamp forests and temporally flooded lake margin**<br>*Sphagnum* sp.<br>*Equisetum* sp.<br>*Osmunda parschlugiana*<br>*Alnus cecropiifolia*<br>aff. Calycanthaceae<br>Chenopodiaceae aff. *Chenopodium* sp.<br>Chenopodiaceae gen. et spec. indet. 1-2<br>Cyperaceae<br>*Decodon* sp.<br>*Parthenocissus* sp.<br>Poaceae gen. et spec. indet. 1<br>*Pterocarya* sp.<br>Ranunculaceae gen. et spec. indet. 1, 2<br>*Salix gruberi*<br>*Smilax* sp. | **Levée forests and well-drained lake margins**<br>*Lycopodium* sp.<br>*Polypodium* sp.<br>Polypodiaceae gen. et spec. indet. 1-4<br>*Acer crenatifolium* subsp. *islandicum*<br>*Alnus cecropiifolia*<br>*Crataegus* sp.<br>*Lonicera* sp. 1-3<br>*Parthenocissus* sp.<br>*Platanus* sp.<br>Poaceae gen. et spec. indet. 1<br>Rosaceae gen. et spec. indet. 1-7<br>*Smilax* sp.<br>*Ulmus* sp. | **Well-drained lowland forests and lake margins**<br>*Equisetum* sp.<br>*Osmunda parschlugiana*<br>*Tsuga* sp.<br>*Acer askelssonii*<br>*Acer crenatifolium* subsp. *islandicum*<br>*Alnus cecropiifolia*<br>*Betula islandica*<br>aff. Calycanthaceae<br>*Carpinus* sp. 2<br>*Corylus* sp.<br>*Crataegus* sp.<br>Cyperaceae<br>Liliaceae gen. et spec. indet. 2-3<br>*Lonicera* sp. 1-3<br>*Parthenocissus* sp.<br>*Platanus* sp.<br>*Pterocarya* sp.<br>*Rhododendron* aff. *ponticum*<br>Rosaceae gen. et spec. indet. 1-7<br>*Trigonobalanopsis* sp. †<br>*Ulmus* sp. | **Rocky outcrop forests**<br>*Lycopodium* sp.<br>*Lycopodiaceae* aff. *Huperzia* sp.<br>*Ginkgo* sp.<br>*Larix* sp.<br>*Picea* section *Picea* sp.<br>*Pinus* sp. 1<br>*Pseudotsuga* sp.<br>*Tsuga* sp.<br>*Plantago lanceolata* type<br>Poaceae gen. et spec. indet. 1<br>Rosaceae gen. et spec. indet. 1-7<br>*Thalictrum* sp. 1 | **Foothill forests**<br>*Lycopodium* sp.<br>*Polypodium* sp.<br>Polypodiaceae gen. et spec. indet. 1-4<br>*Ginkgo* sp.<br>*Pinus* sp. 2<br>*Pseudotsuga* sp.<br>*Tsuga* sp.<br>*Sciadopitys* sp.<br>*Acer askelssonii*<br>*Acer crenatifolium* subsp. *islandicum*<br>*Alnus cecropiifolia*<br>*Betula islandica*<br>*Carpinus* sp. 2<br>cf. *Cyclocarya* sp.<br>*Corylus* sp.<br>*Fagus* sp.<br>*Lonicera* sp. 1, 2<br>*Platanus* sp.<br>*Rhododendron* aff. *ponticum*<br>Rosaceae gen. et spec. indet. 1-7<br>Rosaceae gen. et spec. indet. type A<br>*Tilla* sp.<br>*Trigonobalanopsis* sp. † | **Meadows and shrublands**<br>*Huperzia* sp.<br>*Anemone* sp.<br>Apiaceae gen. et spec. indet. 1-4<br>*Arctostaphylos* sp.<br>*Artemisia* sp. 1, 2<br>Asteraceae gen. et spec. indet. 1-3<br>Caryophyllaceae gen. et spec. indet. 1-3<br>Cyperaceae<br>Poaceae gen. et spec. indet. 1 | **Montane forests**<br>*Lycopodium* sp.<br>*Polypodium* sp.<br>Polypodiaceae gen. et spec. indet. 1-4<br>*Ginkgo* sp.<br>*Abies* sp.<br>*Larix* sp.<br>*Picea* section *Picea* sp.<br>*Pinus* sp. 1<br>*Pseudotsuga* sp.<br>*Tsuga* sp.<br>*Acer crenatifolium* subsp. *islandicum*<br>*Cyclocarya* sp.<br>*Fagus* sp.<br>*Lonicera* sp. 1, 2<br>*Rhododendron* aff. *ponticum*<br>*Sciadopitys* sp.<br>*Tilia* sp.<br>*Ulmus* sp. | **Ravine forests**<br>*Sphagnum* sp.<br>*Osmunda parschlugiana*<br>*Polypodium* sp.<br>Polypodiaceae gen. et spec. indet. 1-4<br>*Abies* sp.<br>*Tsuga* sp.<br>*Calycanthus* sp.<br>*Corylus* sp.<br>*Fagus* sp.<br>Rosaceae gen. et spec. indet. 1-5<br>*Tilia* sp.<br>*Ulmus* sp. |
| **AZONAL VEGETATION** | | | **ZONAL VEGETATION** | | | | | |

The palaeoecology of fossil species is reconstructed from their sedimentological context and ecology of modern analogues

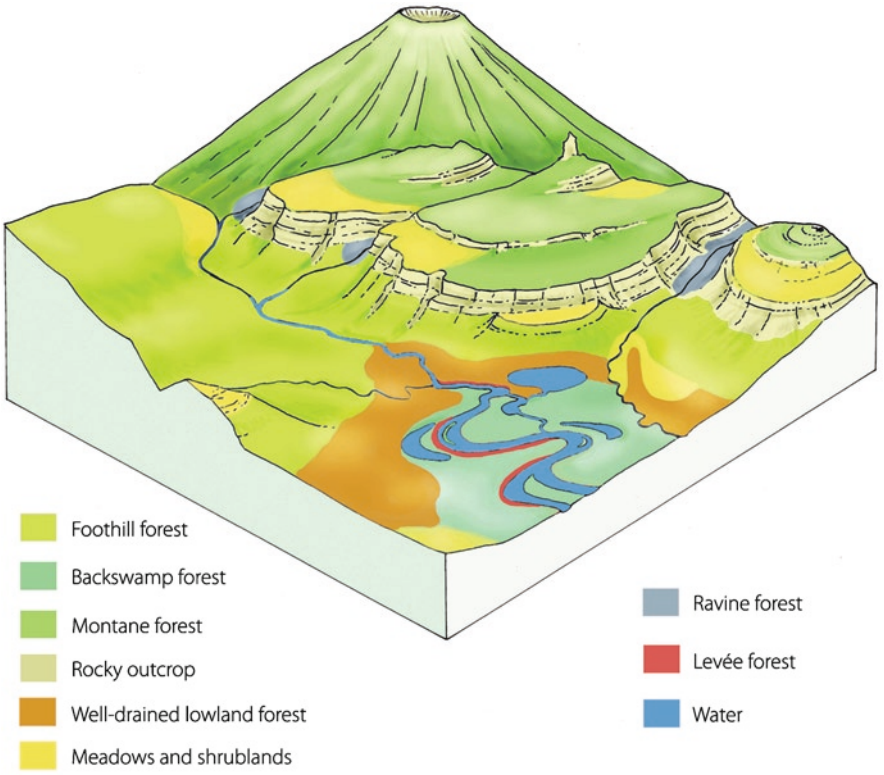



**Fig. 6.3** Schematic block diagram showing palaeo-landscape and vegetation types for the early Late Miocene of Iceland. See Table 6.2 for species composition of vegetation types

Areas with lower ground water tables may have been richer in tree species (*Acer* spp., *Platanus*, Rosaceae etc.) and the diversity of these forests probably further increased towards the well-drained mountain slopes. Evergreen understorey or forest gap elements such as *Rhododendron* aff. *ponticum* and mesophytic trees (*Fagus*, *Tilia*) were characteristic of well-drained forests from the lowlands to higher elevations (Fig. 6.4). Also, the conifer species (including *Ginkgo*) recorded for the 10 Ma formation were most likely elements of these well-drained zonal forests.

The presence of open landscapes is indicated by the substantial amount of herbaceous (including grasses) elements in the palynological record and macrofossils of small-leaved shrubs of small stature most likely belonging to the Ericaceae (*Vaccinium*, *Arctostaphylos*). This is a novel feature of the Icelandic landscape that has not been recorded in the older sedimentary formations (Fig. 6.3). Herbs and grasses formed meadows and were components of shrubland vegetation and rocky outcrop forests on poor soils (Table 6.2; Fig. 6.5). Families represented by herbaceous taxa (Asteraceae, Caryophyllaceae etc.) also play an important role in the modern Icelandic vegetation.

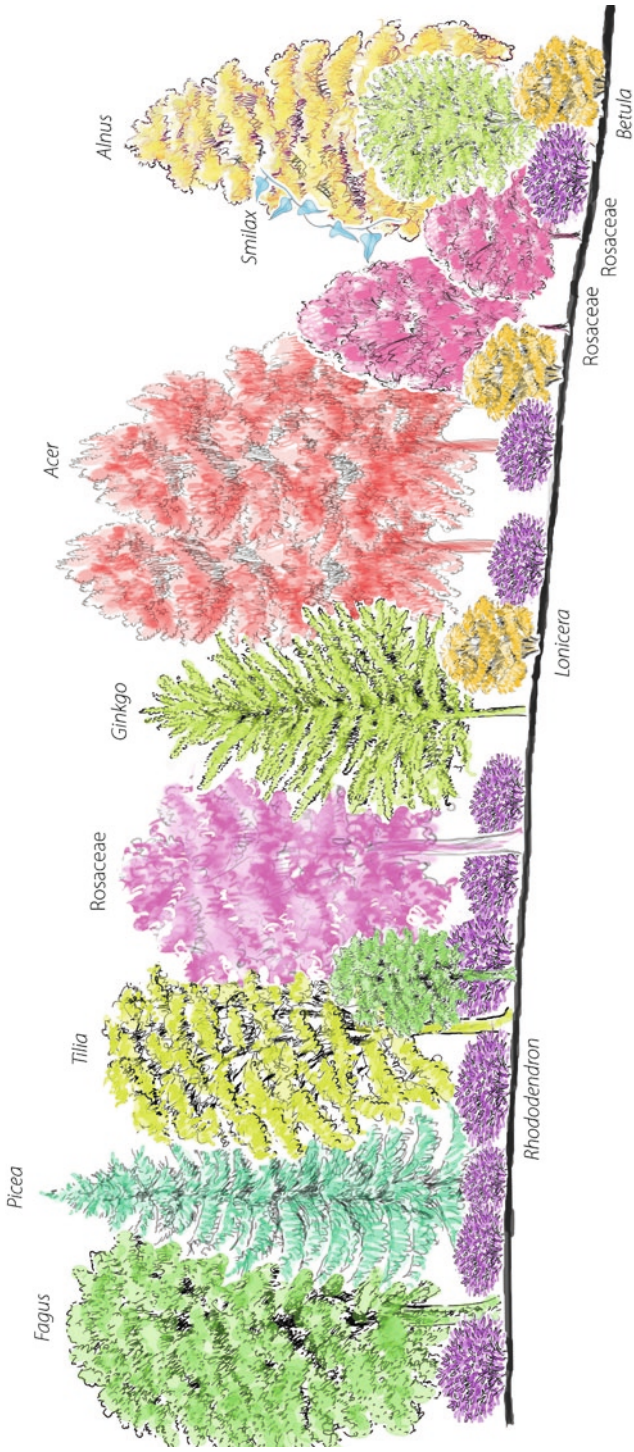



**Fig. 6.4** Schematic transect of a well-drained lowland forest

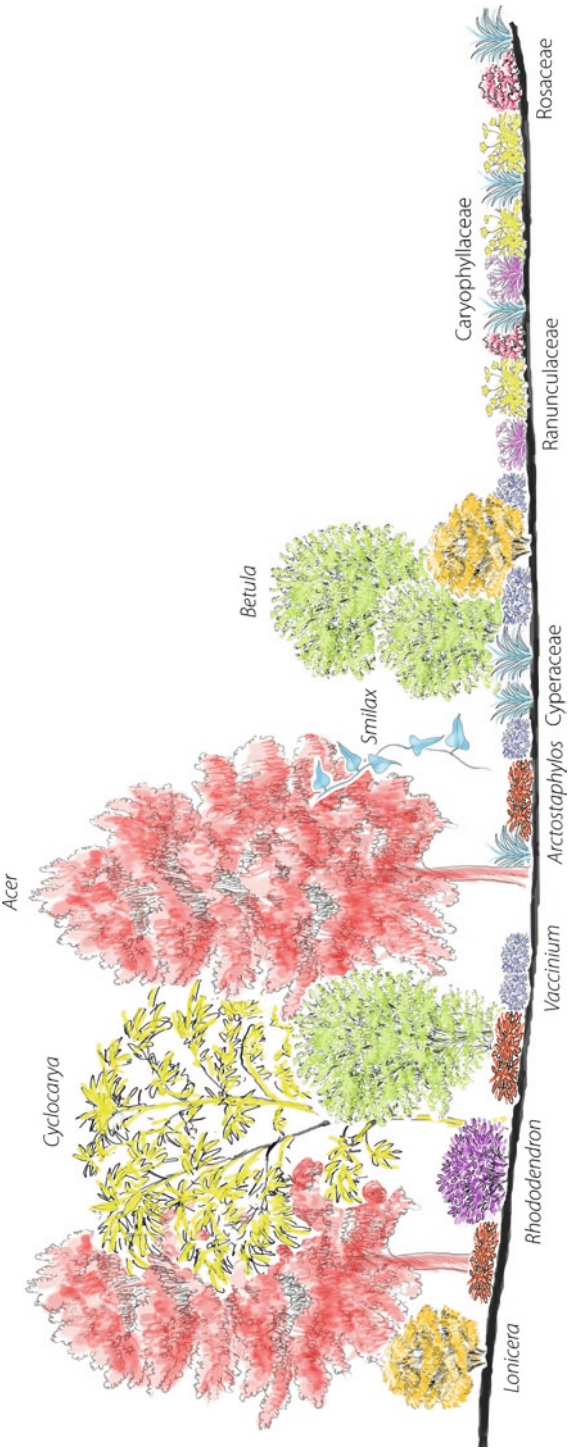



**Fig. 6.5** Schematic transect of diverse vegetation showing well-drained lowland forest, forest edge and meadow

## 6.4 Ecological and Climatic Requirements of Modern Analogues

The taxa recovered from the 10 Ma formation appear to signal a marked change in ecological and climatic conditions as compared to the older (15 and 12 Ma) floras. Warmth-loving conifers (Cupressaceae) and angiosperms (Lauraceae, Magnoliaceae) are absent from the 10 Ma formation and instead shrubs and herbaceous taxa that are typical of cool-temperate conditions are present. Overall, this suggests cooler conditions for the 10 Ma formation and a more diverse vegetation (Fig. 6.3). Climatic properties of all the taxa are listed in Appendix 13.1, Chap. 13; brief descriptions of *Sciadopitys* and *Betula islandica* are given in Chap. 5 and of *Fagus* and *Platanus* in Chap. 4.

*Ginkgo*, the maidenhair tree, is represented by a single living species, *G. biloba* L. that is known in only a few populations in low coastal regions and interior mountains along the Yangtze River in Eastern China. It is not entirely clear whether these populations are in fact natural ones or whether they had been planted by monks. In semi-wild stands, *Ginkgo* grows in disturbed micro-sites, such as stream banks, steep rocky slopes and the edges of exposed cliffs (Del Tredici et al. 1992). In addition, Del Tredici (1989) suggested that *Ginkgo* is a gap opportunist, i.e. a tree that can cope with shady conditions in the understorey until it becomes a canopy tree when a gap occurs. Royer et al. (2003) analysed more than 50 fossil sites with *Ginkgo* ranging in age from the Late Cretaceous to the Middle Miocene, mostly from Arctic areas. Based on sedimentological and floristic context, they concluded that ginkgoes were largely confined to disturbed stream margins and levée environments. In the northern hemisphere, *Ginkgo* shifted from high latitudes to lower latitudes from the Paleocene onward. It became confined to Eurasia by the end of the Miocene (Denk and Velitzelos 2002). In Europe, *Ginkgo* is a very rare element during the Miocene, found as single leaves or leaf fragments (Denk and Velitzelos 2002; Hably and Marrón 2007; Kvaček et al. in press). This situation, and the one in Iceland, may be substantially different from the one reported by Royer et al. (2003) where ginkgoes in many cases are abundant elements of the fossil assemblages. The sparse occurrence of *Ginkgo* in Miocene assemblages of Iceland may indicate it was an element of well-drained (light) forests (cf. Fig. 6.4) at some distance from the area of sedimentation. Extant *Ginkgo biloba* (cultivated) grows in a wide variety of climates, ranging from Mediterranean to cold temperate (Royer et al. 2003).

*Carpinus* comprises about 25 species with a northern hemispheric disjunct distribution (Flora of North America Editorial Committee 1997). Most species occur in eastern Asia and grow in temperate to subtropical mixed forests, often on moist mountain slopes, but also in edaphically dry places (Flora of China Editorial Committee 1999). In China, the vertical distribution of *Carpinus* is from 200 to 2,900 m a. s. l. In North America, a single species, *C. caroliniana* Walter is an element of rich deciduous lowland forests (0–300 m) along stream banks. In western Eurasia, a few species are found in rich lowland forests and in Submediterranean light forests. The genus occurs in a wide range of climates,

mostly in Cfa climates and occasionally in Csa/Cwa climates with MAT 2.5–28.2°C (Thompson et al. 1999).

*Cyclocarya* comprises a single modern species, *C. paliurus* (Batalin) Iljinsk., which is endemic to China. It grows in moist mountain forests from 400 to 2,500 m a. s. l. (Flora of China Editorial Committee 1999) under a Cfa climate with MAT 3.5–20.5°C.

*Decodon* is represented by a single living species, *D. verticillatus* (L.) Elliott, endemic to eastern North America (Florida to Nova Scotia). It is a suffrutescent plant that forms dense stands in shallow water around lakes and *Taxodium-Nyssa* swamp forests (Kvaček and Sakala 2006). This genus had a much wider distribution but similar ecological range during the Tertiary (Kvaček and Sakala 2006). It is clearly an azonal element that is less useful for climate estimates. The modern species mainly occurs in a (warm) temperate humid Cfa climate (extending into Dfb) with MAT 2.1–19.8°C.

*Smilax* from the 10 Ma formation in Iceland is similar to the modern woody vine *S. rotundifolia* L. from eastern North America, which thrives in dry to moist, often riparian forests. This species, and most of the remaining species of the genus that do not occur in a Mediterranean Csa climate, thrive under a warm temperate fully humid Cfa climate with MAT 2.1–19.8°C.

*Tilia* is a typical northern hemisphere temperate tree genus with about 25 species in North America, Europe and Asia. It is a component of well-drained mixed hardwood forests. The European and Asian Minor species *Tilia platyphyllos* typically grows in a Cfb climate with MAT 3.4–14°C. *Tilia americana* L. native of eastern North America occurs in cold to warm temperate Dfb to Cfa/b climates (Kottek et al. 2006) with MAT 1.1–16.1°C (Thompson et al. 2000).

The herbaceous taxa recorded from the Tröllatunga-Gautshamar Formation are not indicative of particular climate types. However, all of them are, among others, elements of modern Arctic-Alpine vegetation types. Similarly, small-leaved types of Ericaceae (*Vaccinium, Arctostaphylos*) presently thrive under various climate types (Cfb to Dfc and ET; Kottek et al. 2006) with MAT from far below the freezing point up to ca 12–14°C (*V. uliginosum* L., *V. vitis-idaea* L., *Arctostaphylos uva-ursi* (L.) Spreng.).

The plant assemblage recovered from the 10 Ma Tröllatunga-Gautshamar Formation indicates diverse environmental conditions reflecting a range of climate types. Lowlands, although devoid of warmth-loving Taxodiaceae, contained *Platanus*, pointing to warm temperate (Cf climates) conditions. Based on the modern distribution of *Platanus*, this genus is limited by temperature (overall warm, no severe winter frosts) rather than precipitation (Nixon and Poole 2003; Cfa and Csa climates according to Köppen). However, the eastern North American *P. occidentalis* L. extends into regions with Dfa and Dfb climates (Thompson et al. 1999). Given the position of Iceland in the northern North Atlantic, a fully humid climate can be assumed for the Miocene. However, mountains of up to 2,000 m provided a barrier to humid air and may have caused more continental conditions in the interior, as is the case today. In an overall warm climatic setting as found in the 15 and 12 Ma time periods, this might have caused only little variation in the vegetation.

Cooler conditions at 10 Ma may have increased the effect of relief, favouring herbaceous and shrubland vegetation. In coastal lowlands and on moist mountain slopes, rich hardwood forests could thrive. The presence of *Fagus* and *Rhododendron ponticum* /*R. maximum* in such forests strongly indicate warm temperate conditions (Cfb climates). Meadows and shrublands could occupy open patches in the forest vegetation because of edaphic differences and outcompeted forest vegetation in drier/cooler places in the interior and at higher elevations (Fig. 6.3). MAT in the 10 Ma formation would have been 8–10°C in lowlands and slightly cooler on moist foothills. Variants of this climate types would have been caused by elevation (cooler) and/or rain shelter in the interior (drier).

## 6.5 Migration Routes and Taxonomic Affinities of Newcomers: Implications for Continuous Land Bridge Availability

For the 10 Ma Tröllatunga-Gautshamar Formation, no clear pattern emerges favouring migration to Iceland from either Europe or North America (Denk et al. 2005; Grímsson and Denk 2007). Most taxa that first arrived in the 10 Ma formation cannot be identified below the genus or even subfamily level. Modern higher taxa, to which the fossils can be assigned, mostly show a Eurasian-North American distribution. Therefore, most of the new taxa could have migrated to Iceland from either North America/Greenland or Europe. Exceptions are *Ginkgo* and the extinct Fagaceous genus *Trigonobalanopsis*.

*Ginkgo* was widespread in the Early Tertiary "Brito-Arctic Igneous Province" (Boulter and Kvaček 1989) in the so-called "Polar Broadleaved Deciduous Forests" (Mai 1995). In North America, the genus persisted until the late Early Miocene (western United States, Eagle Creek Formation, Chaney 1920; Manchester 1999). In contrast, *Ginkgo* persisted in Europe until the Pliocene (Denk and Velitzelos 2002). This may indicate that *Ginkgo* arrived from Europe sometime between 12 and 10 Ma. Little is known about how *Ginkgo* is dispersed. For Mesozoic ginkgoes, it has been suggested that terrestrial reptiles dispersed the large fleshy fruits (Tiffney 1986, 2004), while modern *Ginkgo* is probably dispersed by mammals (Del Tredici et al. 1992).

*Trigonobalanopsis* is an extinct fagaceous genus that was widespread in the European Tertiary from the Eocene to the Late Miocene (Kvaček and Walther 1988; Walther and Zetter 1993). In contrast, it has no known fossil record in North America. The genus formed part of warm temperate mixed mesophytic and broadleaved deciduous forests in the Miocene. By the Late Miocene, *Trigonobalanopsis* had become a rare element in Europe. Thus, available evidence points to the migration of this relict taxon from Europe to Iceland between 12 and 10 Ma. Like *Fagus*, *Trigonobalanopsis* had little potential for long distance dispersal.

*Cyclocarya* is at present confined to mixed mesophytic forests of southeastern China. Unequivocal fossils of winged fruits are known from the Paleocene of North America (Manchester 1999); in Europe and Asia, the genus has a fossil record from the Oligocene to the Late Pliocene (Mai 1995). Leaflets from Tröllatunga assigned to

*Cyclocarya* sp. are very similar to *C. ezoana* (Tanai and N. Suzuki) Wolfe and Tanai from the Middle Miocene Seldovia Point Flora, Alaska (Wolfe and Tanai 1980). *Cyclocarya ezoana* was originally described from the Middle Miocene of Japan (Tanai and Suzuki 1963). Similar types are also known from the Early Miocene of Germany (*C. cyclocarpa* (Schlecht.) Iljinsk.; Budantsev 1994; Mai 1995). Based on the present data, it is difficult to determine whether *Cyclocarya* migrated to Iceland from Europe or North America. A migration route from North America has previously been suggested for *Fagus friedrichii* that has a disjunct distribution in the Middle Miocene of Iceland and the Seldovian Point Flora from Alaska (see Chap. 4; Grímsson and Denk 2005). In view of the close similarity of leaves from the Tröllatunga locality and the late Early/early Middle Miocene Seldovian Point Flora, a migration from North America seems more probable. However, since leaf fossils of *Cyclocarya* are also known from Europe, a migration from the east cannot entirely be ruled out.

*Decodon* is a monotypic genus in eastern North America with a single species, *D. verticillatus*. It is represented by pollen in the Tröllatunga-Gautshamar Formation in Iceland and leaves unambiguously belonging to *Decodon* are known from the Seldovian Point Flora in Alaska (Wolfe and Tanai 1980).The genus was fairly common in Eurasia from the Eocene to the Pliocene and in North America from the Eocene onwards (Manchester 1999). Thus, a particular migration route to Iceland cannot be determined.

Only a few taxa are indicative of a particular migration route of plants to Iceland during the period 12–10 Ma. Of these, *Ginkgo* and *Trigonobalanopsis* are more likely to have colonized Iceland from the east. Neither taxon is dispersed by wind or birds over large distances, which suggests the presence of a functioning North Atlantic land bridge between Europe and Iceland between 12 and 10 Ma (for a definition of "land bridge" see Chap. 12). In contrast, *Cyclocarya* probably reached Iceland from the west. The seeds of *Cyclocarya* are transported by wind over short distances, suggesting a land bridge also for the western link to the American continent via Greenland.

## 6.6 Origin of Herbaceous Vegetation in Iceland

Herbaceous plants are very rare in the fossil record of Iceland prior to 10 Ma (see Chaps. 4, 5). In Europe, families comprising mainly herbaceous taxa become more common in the fossil record partly in the Oligocene (Cyperaceae, Ranunculaceae) but mainly in the course of the Miocene (Asteraceae, Caryophyllaceae, Chenopodiaceae, Rosaceae herbaceous types; Mai 1995). This may be related to more continental conditions originating after the Oligocene (e.g. uplift of the Tibetan Plateau) and general cooling due to the expansion of the Antarctic Ice Sheet (Zachos et al. 2001), which in turn opened up new niches for herbaceous plants and increased the probability of them becoming fossilized. The sudden appearance of herbaceous plants in the global fossil record after the Oligocene does not reflect the evolutionary histories of these plant groups. In fact, many herbaceous lineages originated much earlier (Late Cretaceous, Early Tertiary; cf. Magallón et al. 1999). The more prominent presence in the fossil record is rather due to the increased availability of suitable

niches resulting from tectonic and climatic changes (Zachos et al. 2001). In the same way, the large proportion of herbaceous taxa in the Icelandic fossil record may reflect the opening up of new niches as a result of cooling in the northern North Atlantic (Chap. 13). Changed environmental conditions would have increased the competitiveness of herbaceous plants against more thermophilic woody taxa. Such niches may not have been available during the warm 15 and 12 Ma time intervals.

## 6.7 Comparison to Coeval Northern Hemispheric Floras

The diverse assemblage of the 10 Ma Tröllatunga-Gautshamar Formation shows similarities to a flora from Arctic North America (Lignite Creek Flora, Alaska; Homerian Stage, Usibelli Group, Zone L-1, L-2; Leopold and Liu 1994; White et al. 1997; Appendix 6.1). Both the Icelandic and the Alaskan floras lack warmth-loving conifers belonging to the Cupressaceae s.l. and share several Pinaceous taxa and *Sciadopitys*. A high degree of similarity is also seen among the angiosperms. Taxa in the Lignite Creek flora that are missing in Iceland are Araliaceae, *Castanea*, *Elaeagnus* and *Liquidambar*. In contrast, *Smilax* and *Ginkgo* are recorded in the Icelandic flora but absent from the Alaskan pollen assemblage.

Despite the appreciable similarity between the two floras, the change from the older Middle Miocene floras to the early Late Miocene flora is more pronounced in Iceland than in Alaska. While a major floristic change occurred between 15 and 12 Ma in Arctic North America (see Chap. 5, Appendix 5.1) this change came later in Iceland, between the late Middle Miocene (12 Ma) and early Late Miocene (10 Ma).

Only few early Late Miocene floras are available from North America and western Eurasia. The Achldorf flora (southern Germany; Knobloch 1986; Gregor 1986; Appendix 6.1) is one of the most diverse floras of the "Upper Freshwater Molasse" and may serve as an example for a mid-latitude flora. The flora is slightly older than Tröllatunga (Sarmatian to Pannonian, Central European Mammal Zone MN9; Unger 1986) and is possibly intermediate in age between the 12 Ma and 10 Ma floras of Iceland. A number of genera are shared between the 12 and 10 Ma floras of Iceland and Achldorf (e.g. *Platanus*, *Acer*, various Betulaceae and Fagaceae, *Pterocarya*, *Smilax*, and *Ulmus*). However, genera such as *Acer* and *Quercus* are markedly richer in species. Representatives of the genus *Quercus* mainly belong to the *Quercus* infrageneric group *Cerris* (Denk and Grimm 2009, 2010) which has a more southern distribution than the white (or red) oaks reported from Iceland (Denk et al. 2010). In addition, the warmth-loving Cupressaceae (*Taxodium*), Lauraceae, and Fabaceae distinguish the Achldorf flora from the contemporaneous Icelandic floras.

Overall, the early Late Miocene flora of Iceland represents a diverse vegetation. Broadleaved deciduous forests in Iceland are similar to coeval vegetation types found both in Arctic North America and the mid-latitudes of Europe. Compared to mid-latitude floras in western Eurasia, they are poorer in species and lack several warmth-loving elements. The prominent number of herbaceous taxa and shrubs as seen in Iceland may reflect a stronger response of vegetation to a cooling climate at high latitudes than at mid-latitudes.

## 6.8 Summary

This chapter presents a complete list of taxa for the 10 Ma Tröllatunga-Gautshamar Formation in northwestern Iceland. Compared to the older 12 Ma Brjánslækur-Seljá Formation, the 10 Ma formation is poorer in forest-building tree taxa (both conifers and angiosperms). However, in terms of the total number of taxa (spore, pollen, and macrofossil taxa), this is the most diverse fossil assemblage of Iceland. This diversity mirrors a diversified vegetation, including lowland riparian and well-drained forests, upland forests as well as meadows and shrublands with a markedly "modern" appearance. Many of the new elements recorded for the 10 Ma formation are herbaceous plants that (at the genus level) are also found in the modern vegetation of Iceland. The co-occurrence of humid warm temperate forests containing exotic elements (*Cyclocarya*, *Platanus* etc.) with meadows and shrublands containing taxa that are able to cope with cold conditions (various herbaceous taxa; *Arctostaphylos*, *Vaccinium*) possibly marks a climatic and ecological shift in Iceland in the context of gradual global cooling during this time. Specifically, herbs and small shrubs may have become more competitive at higher elevations and in the interior regions of Iceland due to cooler and/or drier conditions. Migration routes to Iceland were both from the west and the east. A number of taxa not recorded in older formations in Iceland are not dispersed by wind or birds over long distances (*Ginkgo*, *Trigonobalanopsis*, *Cyclocarya*), which is suggestive of an active land bridge between Iceland and the adjacent continents between 12 and 10 Ma.

# Appendix 6.1

Floristic composition of the 10 Ma sedimentary formation of Iceland compared to contemporaneous northern hemispheric mid- and high-latitude floras from North America and western Eurasia.

| **Tröllatunga-Gautshamar flora, Iceland [ca 65°37′N 21°41′W]** 10–9 Ma This study | |
|---|---|
| 3 | Equisetum sp. |
| 1 | Lycopodium sp. |
| 1 | Huperzia sp. |
| 1,3 | Osmunda parschlugiana |
| 1 | Polypodiaceae gen. et spec. indet. 1 |
| 1 | Polypodiaceae gen. et spec. indet. 3 |
| 1 | Polypodiaceae gen. et spec. indet. 4 |
| 1 | Polypodiaceae gen. et spec. indet. 5 |
| 1 | Polypodium sp. 1 |
| 1 | Pteridophyta gen. et spec. indet. 1 |
| 1 | Sphagnum sp. |
| 1 | Ginkgo sp. |
| 1,3 | Larix sp. |
| 1,3 | Picea sect. Picea |
| 1 | Pinus sp. 1 |
| 1 | Pseudotsuga sp. |
| 1 | Sciadopitys sp. |
| 1 | Tsuga sp. 1 |
| 1-3 | Acer askelssonii |
| 1-3 | Acer crenatifolium subsp. islandicum |
| 1-3 | Alnus cecropiifolia |
| 1 | Anemone sp. |
| 1 | Apiaceae gen. et spec. indet. 1-4 |
| 3 | Arctostaphylos sp. |
| 1 | Artemisia sp. 1 |
| 1 | Artemisia sp. 2 |
| 1 | Asteraceae gen. et spec. indet. 1 |
| 1 | Asteraceae gen. et spec. indet. 2 |
| 1 | Asteraceae gen. et spec. indet. 3 |
| 1-3 | Betula islandica |
| 1 | aff. Calycanthaceae |
| 1 | Carpinus sp. |
| 1 | Caryophyllaceae gen et. spec. indet. 1 |
| 1 | Caryophyllaceae gen et. spec. indet. 2 |
| 1 | Caryophyllaceae gen et. spec. indet. 3 |
| 1 | Chenopodiaceae gen et. spec. indet. 1 |
| 1 | Chenopodiaceae gen et. spec. indet. 2 |
| 1 | Chenopodium sp. |
| 1 | Corylus sp. |
| 3 | Cyclocarya sp. |
| 3 | Cyperaceae gen. et spec. indet. A |
| 1 | Decodon sp. |
| 3 | Dicotylophyllum sp. B |
| 3 | Dicotylophyllum sp. C |
| 1 | Ericaceae gen. et spec. indet. 1 |
| 1 | Fagus sp. |
| 1 | Lemnaceae gen. et spec. indet. |
| 1 | Liliaceae gen. et spec. indet. 2 |
| 1 | Liliaceae gen. et spec. indet. 3 |
| 1 | Lonicera sp. 1 |
| 1 | Lonicera sp. 2 |
| 1 | Lonicera sp. 3 |
| 3 | cf. Nuphar sp. |
| 1 | Parthenocissus sp. |
| 1 | Platanus sp. |
| 1 | aff. Plantago lanceolata |
| 1 | Poaceae gen. et spec. indet. 1 |
| 1 | Pollen type 8 |
| 1 | Pollen type 9 |
| 1 | Pollen type 10 |
| 1 | Pollen type 11 |
| 1 | Pollen type 12 |
| 1 | Pollen type 13 |
| 1 | Pollen type 14 |
| 1 | Pollen type 15 |
| 1 | Pollen type 16 |
| 1 | Pollen type 17 |
| 1 | Pollen type 18 |
| 1 | Pollen type 19 |
| 1 | Pollent type 20 |
| 1 | Polygonum sect. Aconogonon sp. |
| 1,3 | Pterocarya sp. |
| 1 | Ranunculaceae gen. et spec. indet. 1 |
| 1 | Ranunculaceae gen. et spec. indet. 2 |

(continued)

| | **Tröllatunga-Gautshamar flora** (continued) |
|---|---|
| 1 | Ranunculus sp. 1 |
| 1-3 | Rhododendron aff. ponticum |
| 1,3 | Rosaceae gen. et spec. indet. type A |
| 1 | Rumex sp. |
| 1,3 | Salix gruberi |
| 1 | Sanguisorba sp. |
| 3 | Smilax sp. |
| 1 | Thalictrum sp. 1 |
| 1 | Tilia sp. |
| 1 | Trigonobalanopsis sp. |
| 1 | Ulmus sp. |
| 3 | Vaccinium sp. |

| | **Lignite Creek flora [ca 64°04′N 148°13′W]**<br>11.3–9.7 Ma<br>(Leopold and Liu 1994; White et al. 1997) |
|---|---|
| 1 | Cyathea sp. |
| 1 | **Lycopodium cf. L. alopecuroides** |
| 1 | **Lycopodium cf. L. complanatum** |
| 1 | **Osmunda sp.** |
| 1 | Selaginella sp. |
| 1 | **Sphagnum sp.** |
| 1 | **Abies cf. A. grandis** |
| 1 | Cedrus sp. |
| 1 | **Larix/Pseudotsuga sp.** |
| 1 | **Picea sp.** |
| 1 | **Pinus sp.** |
| 1 | **Sciadopitys sp.** |
| 1 | **Tsuga cf. canadensis** |
| 1 | **Tsuga cf. heterophylla** |
| 1 | **Tsuga cf. mertensiana** |
| 1 | **Acer sp.** |
| 1 | **Alnus cf. firma** |
| 1 | **Alnus sp.** |
| 1 | **Ambrosia sp.** |
| 1 | Araliaceae |
| 1 | **Artemisia sp.** |
| 1 | **Betula sp.** |
| 1 | **Caprifoliaceae** |
| 1 | Castanea sp. |
| 1 | cf. Crataegus sp. |
| 1 | **Chenopodiineae** |
| 1 | **Compositae** |
| 1 | Cornus sp. |
| 1 | **Corylus sp.** |
| 1 | **Cyclocarya sp.** |
| 1 | Diervilla/Weigelia |
| 1 | Elaeagnus sp. |
| 1 | Ericales indet. |
| 1 | Fraxinus sp. |
| 1 | **Gramineae** |
| 1 | Juglans sp. |
| 1 | Liquidambar sp. |
| 1 | Magnolia sp. |
| 1 | Melia sp. |
| 1 | Onagraceae |
| 1 | **Ostrya/Carpinus sp.** |
| 1 | **Polygonum persicaria** |
| 1 | Populus sp. |
| 1 | **Prunus sp.** |
| 1 | **Pterocarya sp.** |
| 1 | **Pterocarya sp.** |
| 1 | Rhus sp. |
| 1 | **Rosaceae** |
| 1 | **Salix sp.** |
| 1 | Sparganium sp. |
| 1 | **Thalictrum sp.** |
| 1 | **Tilia sp.** |
| 1 | **Ulmus/Zelkova sp.** |

| | **Achldorf flora [48°25′N 12°21′E]**<br>MN8, MN9 (Unger 1986;<br>Knobloch 1986; Gregor 1986; Schmitt 1986) |
|---|---|
| 3 | **Pinus sp.** |
| 2 | **Pinus aff. thomasiana** |
| 3 | Taxodium dubium |
| 2 | Taxodium hantkei |
| 3 | **?Platanus leucophylla** |
| 3 | **Acer cf. ginnala** |
| 3 | **Acer integrilobum** |
| 2 | Acer jurenaky vel pseudoplatanus |
| 2 | **Acer cf. monspessulanum vel italium** |
| 2,3 | **Acer tricuspidatum** |
| 2 | **Acer sp.** |
| 3 | **Alnus alnoidea** |
| 2 | **Alnus kefersteinii** |
| 3 | **Alnus menzelii** |
| 2 | Amentiferae |
| 3 | **Betula subpubescens** |
| 2 | **Betula cf. longisquamosa** |
| 2,3 | **Carpinus cf. grandis** |
| 2 | **Carpinus kisseri** |
| 3 | Carya aff. serraefolia |

(continued)

| | **Achldorf flora** (continued) |
|---|---|
| 3 | Carya minor |
| 2,3 | Carya sp. |
| 3 | Cephalotaxus cf. stockleinea |
| 2 | cf. Clematis vitalba |
| 2 | aff. Corylopsis urselensis |
| 3 | Crataegus cf. neckerae |
| 3 | **Cyperaceae vel Poaceae** |
| 3 | Daphnogene bilinica |
| 3 | Dicotylophyllum cf. oeningense |
| 3 | Dicotylophyllum sp. 1-7 |
| 3 | cf. Diospyros aff. pannonica |
| 3 | cf. Ficus truncata |
| 3 | Gleditsia lyelliana |
| 2 | Gleditsia knorrii |
| 3 | Hemiptelea vel Zelkova sp |
| 2 | Leguminocarpum sp. |
| 3 | Liquidambar europaea |
| 2 | Liquidambar cf. magniloculata |
| 3 | Myrica lignitum |
| 2 | Myrica ceriferiformis |
| 2 | Nymphaea sp. |
| 2 | Ostrya scholzii |
| 2 | Ostrya sp. |
| 2 | Paliurus thurmanni |
| 3 | Palirus tiliaefolius |
| 3 | Parrotia pristina |
| 2 | **Pterocarya limburgensis** |
| 2 | Quercus cerrisaecarpa |
| 3 | Quercus gregori |
| 3 | Quercus cf. kubinyi |
| 3 | Quercus kucerae |
| 3 | Quercus pontica-miocenica |
| 3 | Quercus pseudocastanea |
| 2 | Quercus sapperi |
| 3 | Quercus schoetzii |
| 3 | Quercus sp. |
| 3 | Robinia regeli |
| 2 | Rubus sp. |
| 3 | **Salix sp.** |
| 3 | **Smilax sp. 1-2** |
| 2 | cf. Symplocos lignitarum |
| 2 | Trapa cf. heeri |
| 3 | **Ulmus pyramidalis** |
| 3 | Zelkova praelonga |
| 2 | Zelkova cf. ungeri |
| 2 | Zelkova sp. |

Boldface indicates that the genus is present in the Tröllatunga-Gautshamar Formation. Grey shading indicates that the genus is present in the older Brjánslækur-Seljá Formation (12 Ma) or the younger Skarðsströnd-Mókollsdalur Formation (9–8 Ma). *1* based on pollen, spores; *2* based on leaves and/or fruit/seed fossils; *3* based on leaf fossils.

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## Explanation of Plates

**Plate 6.1** **1**. Húsavíkurkleif and **2**. Tröllatunga (Grýlufoss) in Steingrímsfjörður, northwestern Iceland, Tröllatunga-Gautshamar Formation (ca 10 Ma). **3**. View of the Húsavíkurkleif outcrop, section composed of brownish to reddish iron-rich siltstones and sandstones, with lignite seams and volcanic tephra layers. **4**. Thick pyroclastic pumice rich sedimentary rock unit characteristic for the Tröllatunga outcrops. **5**. The iron-rich sedimentary rock unit at Húsavíkurkleif, fossils found here in concretions. **6**. Close-up showing parts of lignified stems in the white pyroclastic unit found in the Tröllatunga region. **7**. Fossil preserved in brownish to reddish iron-rich concretion from the Húsavíkurkleif outcrop. **8**. Whorl of leaves (distal part of *Rhododendron* branch) preserved in the white pyroclastic unit of the Tröllatunga outcropsv

**Plate 6.2** **1**–**3**. *Huperzia* sp. **1**. Spore in SEM, proximal polar view showing trilete tetrad mark. **2**. Detail of spore surface. **3**. Spore in LM, polar view. **4**–**6**. Polypodiaceae gen. et spec. indet. 1. **4**. Spore in SEM, proximal polar view showing monolete tetrad mark. **5**. Detail of spore surface. **6**. Spore in LM, polar view showing monolete tetrad mark. **7**–**9**. *Sphagnum* sp. **7**. Spore in SEM, distal polar view. **8**. Detail of spore surface. **9**. Spore in LM, polar view showing trilete tetrad mark. **10**–**12**. *Sphagnum* sp. **10**. Spore in SEM, proximal polar view showing trilete tetrad mark. **11**. Detail of spore surface. **12**. Spore in LM, polar view showing trilete tetrad mark

**Plate 6.3** **1**. Bryophyta fam. et gen. indet., acrocarpous moss with numerous stems (S 106487). **2**. Detail of Fig. 1 showing two stems with spirally arranged leaves. **3**, **5** and **7**. *Lycopodium* sp. **3**. Spore in SEM, distal polar view. **5**. Spore in LM, polar view. **7**. Detail of spore surface. **4** and **6**. *Lycopodium* sp. **4**. Spore in SEM, proximal polar view showing trilete tetrad mark. **6**. Spore in LM, polar view. **8**, **10** and **12**. *Lycopodium* sp. **8**. Detail of spore surface. **10**. Spore in SEM, proximal polar view. **12**. Spore in LM, polar view. **9**, **11** and **13**. *Lycopodium* sp. **9**. Detail of spore surface. **11**. Spore in SEM, proximal polar view showing trilete tetrad mark. **13**. Spore in LM, polar view

**Plate 6.4** **1**–**3**. *Huperzia* sp. **1**. Spore in SEM, distal polar view. **2**. Detail of spore surface. **3**. Spore in LM, proximal polar view showing trilete tetrad mark. **4**–**6**. *Huperzia* sp. **4**. Spore in SEM, equatorial view. **5**. Detail of spore surface. **6**. Spore in LM, oblique polar view. **7**–**9**. *Huperzia* sp. **7**. Spore in SEM, distal polar view. **8**. Detail of spore surface. **9**. Spore in LM, proximal polar view showing trilete tetrad mark. **10**–**12**. *Osmunda* sp. **10**. Spore in SEM, proximal polar view showing trilete tetrad mark. **11**. Detail of spore surface. **12**. Spore in LM, polar view

**Plate 6.5** **1**, **2** and **7**. *Osmunda* sp. **1**. Spore in SEM, proximal polar view showing trilete tetrad mark. **2**. Detail of spore surface. **7**. Spore in LM, polar view. **3**, **4** and **8**. *Osmunda* sp. **3**. Spore in

SEM, distal polar view. **4**. Detail of spore surface. **8**. Spore in LM, proximal polar view showing trilete tetrad mark. **5** and **6**. *Osmunda* sp. **5**. Spore in SEM, oblique proximal polar view. **6**. Detail of spore surface. **9** and **10**. *Osmunda* sp. **9**. Spore in SEM, proximal polar view showing trilete tetrad mark. **10**. Detail of spore surface

**Plate 6.6** **1**. *Osmunda parschlugiana*, leaf with alternately arranged pinnae (S 106766). **2**. *Osmunda parschlugiana*, lower part of pinna with a wide base (IMNH). **3**. Detail of Fig. 1 showing venation and branching towards margin. **4**. *Osmunda parschlugiana*, distal part of leaf with densely spaced small pinnae (IMNH). **5**. *Osmunda parschlugiana*, large pinna with numerous secondary veins (IMNH). **6**. Pteridophyta gen. et spec. indet 1., leaf fragment. **7**. Detail of Fig. 6 showing pinnae. **8**. *Equisetum* sp., nodules (IMNH 5547). **9**. *Equisetum* sp., rhizome/stem part (IMNH)

**Plate 6.7** **1** and **3**. *Polypodium* sp. **1**. Monolete spore in SEM, equatorial view. **2**. Spore in LM, equatorial view. **3–5**. Polypodiaceae gen. et spec. indet 1. **3**. Spore in SEM, equatorial view. **4**. Detail of spore surface. **5**. Spore in LM, proximal polar view showing monolete tetrad mark. **6–8**. Polypodiaceae gen. et spec. indet 3. **6**. Monolete spore in SEM, equatorial view. **7**. Detail of spore surface. **8**. Spore in LM, equatorial view. **9–11**. Polypodiaceae gen. et spec. indet 4. **9**. Monolete spore in SEM, equatorial view. **10**. Detail of spore surface. **11**. Spore in LM, equatorial view. **12–14**. Polypodiaceae gen. et spec. indet 5. **12**. Monolete spore in SEM, equatorial view. **13**. Detail of spore surface. **14**. Spore in LM, equatorial view

**Plate 6.8** **1–3**. *Ginkgo* sp. **1**. Pollen grain in SEM. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM. **4**. *Larix* sp., long shoot with short lateral spur shots. **5**. Detail of Fig. 4 showing section through a spur shot. **6**. Detail of Fig. 4 showing short spur shot. **7**. *Pseudotsuga* sp., female cone. **8–10**. *Larix*/*Pseudotsuga* sp. **8**. Pollen grain in SEM. **9**. Detail of pollen grain surface. **10**. Pollen grain in LM

**Plate 6.9** **1**. *Sequoia abietina* (Brongn.) Knobl., shoot with leaves (IMNH). **2**. *Sequoia abietina* (Brongn.) Knobl., shoot with leaves (IMNH). **3**. *Picea* sp., long shoot with raised scars indicating fallen leaves (S 106739). **4**. Detail of Fig. 3 showing raised scars. **5**. *Picea* sp., needle like leaf with truncate base (IMNH 2832-04). **6**. *Picea* sp., needle like leaf with truncate base (IMNH 259). **7**. *Picea* sp., needle like leaf with acute apex (S 106487). **8**. *Picea* sp., needle like leaf with truncate base (IMNH 1960-03)

**Plate 6.10** **1–5**. *Picea* sp. **1**. Bisaccate pollen grain in SEM, equatorial view. **2** and **3**. Bisaccate pollen grain in LM, equatorial view. **4**. Detail of corpus. **5**. Detail of saccus. **6**. *Picea* sp., male catkins with *Picea* sp. pollen *in situ* (S106517A). **7**. Detail of Fig. 6 showing widely spaced microsporophylls. **8**. *Picea* sp. pollen grain from catkin in Fig. 6., pollen grain in LM, equatorial view. **9–12**. *Pinus* sp. 1 (Diploxylon type). **9**. Bisaccate pollen grain in SEM, equatorial view. **10**. Detail of corpus. **11** and **12**. Pollen grain in LM, oblique equatorial view

**Plate 6.11** **1–3**. *Tsuga* sp.1. **1**. Monosaccate pollen grain in SEM. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM. **4–6**. *Sciadopitys* sp. **4**. Pollen grain in SEM, proximal polar view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, distal polar view. **7**, **9** and **10**. *Sciadopitys* sp. **7**. Pollen grain in SEM, proximal polar view. **9**. Detail of pollen grain surface. **10**. Pollen grain in LM, polar view. **8** and **11**. Sciadopitys sp. **8**. Pollen grain in SEM, distal polar view. **11**. Pollen grain in LM, polar view

**Plate 6.12** **1–4**. Apiaceae gen. et spec. indet. 1. **1**. Pollen grain in SEM, equatorial view. **2**. Pollen grain in LM, equatorial view. **3**. Detail of pollen grain surface around porus. **4**. Detail of pollen grain surface in polar area. **5** and **6**. Apiaceae gen. et spec. indet. 2. **5**. Pollen grain in SEM, equatorial view. **6**. Pollen grain in LM, equatorial view. **7–9**. Apiaceae gen. et spec. indet. 3. **7**. Pollen

grain in SEM, equatorial view. **8**. Pollen grain in LM, equatorial view. **9**. Detail of pollen grain surface in polar area. **10–13**. Apiaceae gen. et spec. indet. 4. **10**. Pollen grain in SEM, equatorial view. **11**. Pollen grain in LM, equatorial view. **12**. Detail of pollen grain surface in polar area. **13**. Detail of pollen grain surface around porus

**Plate 6.13** **1–4**. *Artemisia* sp. 1. **1**. Pollen grain in SEM, polar view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4**. Pollen grain in LM, polar view. **5–7**. *Artemisia* sp. 2. **5**. Pollen grain in SEM, equatorial view. **6**. Detail of pollen grain surface. **7**. Pollen grain in LM, equatorial view. **8–10**. *Artemisia* sp. 2. **8**. Pollen grain in SEM, equatorial view. **9**. Detail of pollen grain surface. **10**. Pollen grain in LM, polar view

**Plate 6.14** **1–3**. Asteraceae gen. et spec. indet. 1 (Liguliflorae). **1**. Pollen grain in SEM, polar view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, polar view. **4–6**. Asteraceae gen. et spec. indet. 2. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7–9**. Asteraceae gen. et spec. indet. 2. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view. **10–12**. Asteraceae gen. et spec. indet. 3. **10**. Pollen grain in SEM, polar view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, polar view

**Plate 6.15** **1**. *Alnus cecropiifolia*, large wide elliptic leaf (S 087416). **2**. Detail of Fig. 1 showing teeth and marginal venation. **3**. *Alnus cecropiifolia*, elliptic leaf with round base (IMNH 3179). **4**. *Alnus kefersteinii*, female infructescence (S 106556). **5**. *Alnus kefersteinii*, female infructescence (IMNH). **6**. *Alnus kefersteinii*, female infructescence (IMNH)

**Plate 6.16** **1–3**. *Alnus* sp. 1. **1**. Pollen grain in SEM, polar view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, polar view. **4–6**. *Alnus* sp. 1. **4**. Pollen grain in SEM, polar view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, polar view. **7–9**. *Alnus* sp. 2. **7**. Pollen grain SEM, polar view. **8**. Detail of pollen grain surface. **9**. Pollen grain LM, polar view. **10–12**. *Alnus* sp. 3. **10**. Pollen grain in SEM, polar view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, polar view. **13–15**. *Alnus* sp. 3. **13**. Pollen grain in SEM, polar view. **14**. Detail of pollen grain surface. **15**. Pollen grain in LM, polar view

**Plate 6.17** **1–3**. *Betula* sp. **1**. Pollen grain in SEM, polar view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, polar view. **4–6**. *Betula* sp. **4**. Pollen grain in SEM, polar view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, polar view. **7–9**. *Carpinus* sp. 2. **7**. Pollen grain in SEM, polar view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, polar view. **10–12**. Carpinus sp. 2. **10**. Pollen grain in SEM, polar view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, polar view. **13–15**. *Corylus* sp. **13**. Pollen grain in SEM, polar view. **14**. Detail of pollen grain surface. **15**. Pollen grain in LM, polar view

**Plate 6.18** **1–3**. aff. Calycanthaceae **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4–6**. aff. Calycanthaceae **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grains surface. **6**. Pollen grain in LM, equatorial view. **7–9**. aff. Calycanthaceae **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view. **10–12**. aff. Calycanthaceae **10**. Pollen grain in SEM, equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, equatorial view

**Plate 6.19** **1–3**. *Lonicera* sp. 1. **1**. Pollen grain in SEM, polar view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, polar view. **4–6**. *Lonicera* sp. 1. **4**. Pollen grain in SEM, oblique equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, oblique view. **7**, **8** and **12**. *Lonicera* sp. 2. **7**. Pollen grain in SEM, oblique view. **8**. Detail of pollen grain surface. **12**. Pollen

grain in LM. **9**–**11**. *Lonicera* sp. 3. **9**. Pollen in SEM, polar view. **10**. Detail of pollen grain surface. **11**. Pollen grain in LM, polar view

**Plate 6.20** **1**–**3**. Caryophyllaceae gen. et spec. indet. 1. **1**. Pollen grain in SEM. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM. **4**–**6**. Caryophyllaceae gen. et spec. indet. 1. **4**. Pollen grain in SEM. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM. **7**–**9**. Caryophyllaceae gen. et spec. indet. 1. **7**. Pollen grain in SEM. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM. **10**–**12**. Caryophyllaceae gen. et spec. indet. 3. **10**. Pollen grain in SEM. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM

**Plate 6.21** **1**–**4**. Caryophyllaceae gen. et spec. indet. 2. **1**. Pollen grain in SEM. **2**. Detail of pollen grain surface showing porus. **3**. Detail of pollen grain surface around porus. **4**. Pollen grain in LM. **5**–**7**. *Thalictrum* sp. 1. **5**. Pollen grain in SEM. **6**. Detail of pollen grain surface. **7**. Pollen grain in LM. **8**–**10**. *Thalictrum* sp.1. **8**. Pollen grain in SEM. **9**. Detail of pollen grain surface. **10**. Pollen grain in LM

**Plate 6.22** **1**–**3**. *Chenopodium* sp. **1**. Pollen grain in SEM. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM. **4**–**6**. Chenopodiaceae gen. et spec. indet 1. **4**. Pollen grain in SEM. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM. **7**–**9**. Chenopodiaceae gen. et spec. indet. 2. **7**. Pollen grain in SEM. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM

**Plate 6.23** **1**. Cyperaceae gen. et spec. indet. A, leaf fragment (S 094580). **2**. *Arctostaphylos* sp., small leaf (S 106768). **3**. Detail of Fig. 3 showing secondary venation and teeth along margin. **4**. *Vaccinium* sp., elliptic leaf (S 106624). **5**. *Vaccinium* sp., elliptic leaf with dentate margin (S 106621). **6**. *Vaccinium* sp., detail showing small teeth along margin (S 106759). **7**. *Vaccinium* sp., detail showing secondary venation and teeth along margin (S 106624)

**Plate 6.24** **1**–**3**. *Rhododendron* aff. *ponticum* **1**. Medium sized narrow elliptic leaf (S 087459). **2**. Medium sized narrow elliptic leaf (S 106760). **3**. Small narrow elliptic leaf (S 106740). **4**–**6**. *Rhododendron* sp., bud scales

**Plate 6.25** **1**, **3** and **5**. Ericaceae gen. et spec. indet. 1. **1**. Tetrad in SEM. **3**. Detail of tetrad surface. **5**. Tetrad in LM. **2**, **4** and **6**. Ericaceae gen. et spec. indet. 1. **2**. Tetrad in SEM. **4**. Detail of tetrad surface. **6**. Tetrad in LM

**Plate 6.26** **1**–**4**. *Rhododendron* sp. 2. **1**. Tetrad in SEM. **2**. Detail of tetrad surface close to apertures. **3**. Detail of tetrad surface in mesocolpium. **4**. Tetrad in LM. **5**–**8**. *Rhododendron* sp. 2. **5**. Tetrad in SEM. **6**. Detail of tetrad surface. **7**. Tetrad in LM. **8**. Detail showing origin of viscin threads

**Plate 6.27** **1**–**4**. *Fagus* sp. **1**. Pollen in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4**. Pollen grain in LM, polar view. **5**–**7**. *Trigonobalanopsis* sp. **5**. Pollen in SEM, equatorial view. **6**. Detail of pollen grain surface. **7**. Pollen grain in LM, equatorial view. **8**–**10**. *Trigonobalanopsis* sp. **8**. Pollen grain in SEM, equatorial view. **9**. Detail of pollen grain surface. **10**. Pollen grain in LM, oblique equatorial view

**Plate 6.28** **1**. *Pterocarya* sp., medium sized leaflet with asymmetric base (IMNH). **2**. *Cyclocarya* sp., medium sized wide elliptic leaflet (S 106722 A). **3**. *Cyclocarya* sp., counterpart to specimen on Fig. 2 (S 106722 B). **4**. *Cyclocarya* sp., large elliptic leaflet (S 106525). **5**. Detail of Fig. 4 showing secondary venation, looping and branching towards margin. **6**. Detail of Fig. 4 showing teeth along margin

**Plate 6.29** **1–3**. *Pterocarya* sp. **1**. Pollen grain in SEM, polar view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, polar view. **4–6**. *Pterocarya* sp. **4**. Pollen grain in SEM, polar view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, polar view. **7–10**. Liliaceae gen. et spec. indet. 3. **7**. Pollen grain in SEM, distal polar view. **8**. Detail of pollen grain surface showing reticulate sculpturing. **9**. Detail of pollen grain surface showing a more closed tectum. **10**. Pollen grain in LM, distal polar view

**Plate 6.30** **1–3**. Liliaceae gen. et spec. indet. 2. **1**. Pollen grain in SEM, proximal polar view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, polar view. **4–7**. Liliaceae gen. et spec. indet. 3. **4**. Pollen grain in SEM, oblique equatorial view. **5**. Detail of pollen grain surface close to sulcus. **6**. Pollen grain in LM, distal polar view showing sulcus. **7**. Detail of pollen grain surface at proximal polar area

**Plate 6.31** **1–3**. *Decodon* sp. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4–6**. *Decodon* sp. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7–9**. *Decodon* sp. **7**. Pollen grain SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view. **10–12**. *Decodon* sp. **10**. Pollen grain in SEM, equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM

**Plate 6.32** **1**. cf. *Nuphar* sp., part of large round leaf (S 106711). **2**. Detail of Fig. 1 showing venation. **3–6**. aff. *Plantago lanceolata*. **3**. Pollen grain in SEM. **4**. Detail of pollen grain surface. **5**. Pollen grain in LM. **6–8**. *Platanus* sp. **6**. Pollen grain in SEM, equatorial view. **7**. Detail of pollen grain surface. **8**. Pollen grain in LM, equatorial view. **9–11**. *Rumex* sp. **9**. Pollen grain in SEM, polar view. **10**. Detail of pollen grain surface. **11**. Pollen grain in LM, equatorial view

**Plate 6.33** **1**. *Phragmites* sp., rhizomes (IMNH). **2**. *Phragmites* sp., part of leaves (IMNH org 127). **3–5**. Poaceae gen. et spec. indet. 1. **3**. Pollen grain in SEM. **4**. Detail of pollen grain surface. **5**. Pollen grain in LM. **6–8**. Poaceae gen. et spec. indet. 1. **6**. Pollen grain in SEM. **7**. Detail of pollen grain surface. **8**. Pollen grain LM. **9–11**. *Anemone* sp. **9**. Pollen grain in SEM, equatorial view. **10**. Detail of pollen grain surface. **11**. Pollen grain in LM, equatorial view

**Plate 6.34** **1–3**. Ranunculaceae gen. et spec. indet 1. **1**. Pollen grain in SEM, polar view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, polar view. **4–6**. Ranunculaceae gen. et spec. indet 2. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7–9**. Ranunculaceae gen. et spec. indet 2. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view. **10–12**. *Ranunuclus* sp.1. **10**. Pantocolpate pollen grain in SEM. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM. **13–15**. *Polygonum* sect. *Aconogonon* sp. **13**. Pantoporate pollen grain in SEM. **14**. Detail of pollen grain surface. **15**. Pollen grain in LM

**Plate 6.35** **1**. Rosaceae gen. et spec. indet. type A, small elliptic leaf with a long petiole (S 106524). **2**. Detail of Fig. 1 showing venation and teeth along margin. **3–6**. Rosaceae gen. et spec. indet. 3. **3**. Pollen grain in SEM, equatorial view. **4**. Detail of pollen grain surface. **5**. Pollen grain in LM, polar view. **6**. Pollen grain in LM, equatorial view. **7–9**. Rosaceae gen. et spec. indet. 3. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view. **10–12**. Rosaceae gen. et spec. indet. 3. **10**. Pollen grain in SEM, polar view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, polar view

**Plate 6.36** **1–3**. Rosaceae gen. et spec. indet. 4. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4–7**. Rosaceae gen. et spec. indet. 5. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM,

polar view. **7**. Pollen grain LM, equatorial view. **8**–**11**. Rosaceae gen. et spec. indet. 6. **8**. Pollen grain in SEM, equatorial view. **9**. Detail of pollen grain surface. **10**. Pollen grain in LM, polar view. **11**. Pollen grain in LM, equatorial view. **12**–**14**. Rosaceae gen. et spec. indet. 7. **12**. Pollen grain in SEM, equatorial view. **13**. Detail of pollen grain surface. **14**. Pollen grain in LM, equatorial view

**Plate 6.37** **1**–**3**. Rosaceae, unassigned pollen grain. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4**–**6**. Rosaceae, unassigned pollen grain. **4**. Pollen grain in SEM, oblique equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7**–**9**. Rosaceae, unassigned pollen grain. **7**. Pollen grain in SEM, oblique polar view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, oblique polar view. **10**–**12**. *Crataegus* sp. **10**. Pollen grain in SEM, equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, equatorial view

**Plate 6.38** **1**–**3**. Rosaceae gen. et spec. indet. 8. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4**–**6**. Rosaceae gen. et spec. indet. 9. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7**–**9**. *Sanguisorba* sp. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view. **10**–**12**. *Sanguisorba* sp. **10**. Pollen grain in SEM, polar view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, polar view

**Plate 6.39** **1**. *Salix gruberi*, part of leaf (S 094633). **2**–**4**. *Salix* sp. 2. **2**. Pollen grain in SEM, equatorial view. **3**. Detail of pollen grain surface. **4**. Pollen grain in LM, equatorial view. **5**–**7**. *Salix* sp. 3. **5**. Pollen grain in SEM, equatorial view. **6**. Detail of pollen grain surface. **7**. Pollen grain in LM, equatorial view. **8**–**10**. *Salix* sp. 3. **8**. Pollen grain in SEM, equatorial view. **9**. Detail of pollen grain surface. **10**. Pollen grain in LM, equatorial view. **11**–**13**. *Salix* sp. 3. **11**. Pollen grain in SEM, equatorial view. **12**. Detail of pollen grain surface. **13**. Pollen grain in LM, equatorial view

**Plate 6.40** **1**. *Acer askelssonii*, part of large 7 lobed leaf (IMNH). **2**. *Acer askelssonii*, small 3 lobed leaf (S 094385). **3**. *Acer askelssonii*, part of large samara showing the pericarp, arrows pointing to attachment scar (S 106898). **4**. *Acer crenatifolium* subsp. *islandicum*, medium sized 5 lobed leaf (S 087458). **5**. *Acer crenatifolium* subsp. *islandicum*, small 3 lobed leaf (S 106774). **6**. *Acer crenatifolium* subsp. *islandicum*, samara (S 106710). **7**. *Acer crenatifolium* subsp. *islandicum*, samara with complete pericarp and wing (S 106717). **8**. *Acer crenatifolium* subsp. *islandicum*, samara (S 106715). **9**. *Acer crenatifolium* subsp. *islandicum*, attached samaras with a long pedicel (S 106580)

**Plate 6.41** **1**–**3**. *Acer* sp. 1. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4**–**6**. *Acer* sp. 3. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7**, **10** and **14**. *Acer* sp. 4. **7**. Pollen grain in SEM, equatorial view. **10**. Detail of pollen grain surface. **14**. Pollen grain in LM, equatorial view. **8**, **11** and **12**. *Acer* sp. 4. **8**. Pollen grain in SEM, equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, equatorial view. **9** and **13**. *Acer* sp. 4. **9**. Pollen grain in SEM, equatorial view. **13**. Detail of pollen grain surface

**Plate 6.42** **1**. *Smilax* sp., upper half of leaf (S 106746). **2**. Detail of Fig. 1 showing venation and entire margin. **3**. *Smilax* sp., apical part of leaf (S 106749). **4**. Dicotylophyllum sp. C, small elliptic leaf with spinose teeth (S 106780). **5**. Detail of Fig. 4 showing teeth along margin. **6**. Dicotylophyllum sp. B, fragment of leaf (S 106673). **7**. Detail of Fig. 6 showing glandular teeth

**Plate 6.43** **1**–**3**. *Tilia* sp. **1**. Pollen grain in SEM, polar view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, polar view. **4**–**6**. *Ulmus* sp. **4**. Pollen in SEM, polar view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, polar view. **7**–**9**. *Parthenocissus* sp. 7. Pollen grain in SEM,

equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view. **10–12**. *Parthenocissus* sp. **10**. Pollen grain in SEM, equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, equatorial view

**Plate 6.44** **1–3**. Pollen type 8. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4–6**. Pollen type 9. **4**. Pollen grain in SEM. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7–9**. Pollen type 10. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain LM, equatorial view. **10–13**. Pollen type 11. **10**. Pollen grain in SEM, oblique equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, polar view. **13**. Pollen grain in equatorial view

**Plate 6.45** **1–3**. Pollen type 12. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4–6**. Pollen type 13. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7–9**. Pollen type 13. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view. **10–12**. Pollen type 14. **10**. Pollen grain in SEM, equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, equatorial view

**Plate 6.46** **1–3**. Pollen type 15. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4–6**. Pollen type 16. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7–9**. Pollen type 17. **7**. Pollen grain in SEM. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM. **10–12**. Pollen type 18. **10**. Pollen grain in SEM, oblique polar view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, equatorial view

**Plate 6.47** **1–3**. Pollen type 19. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4–6**. Pollen type 20. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view

# Plates




**Plate 6.1**

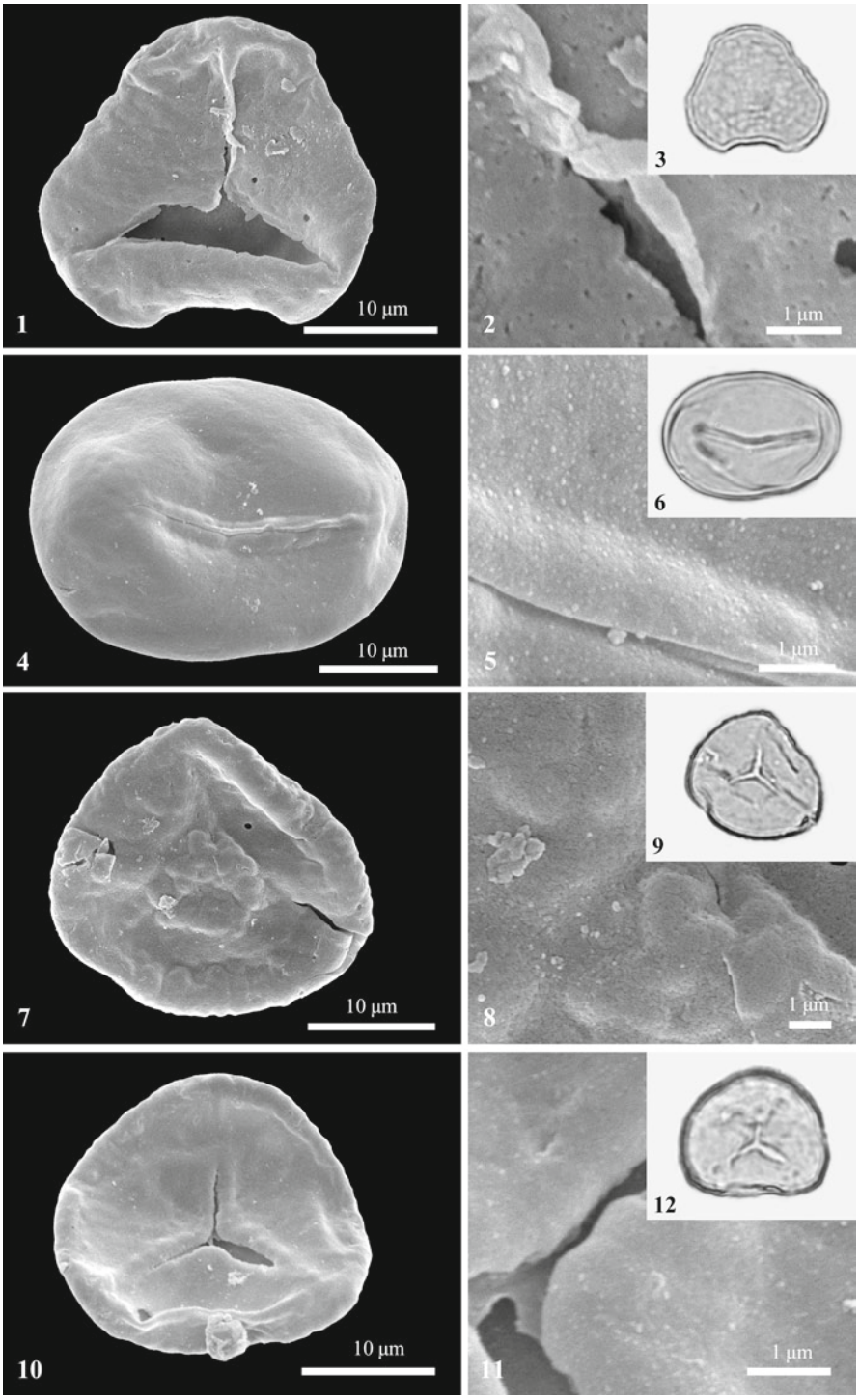



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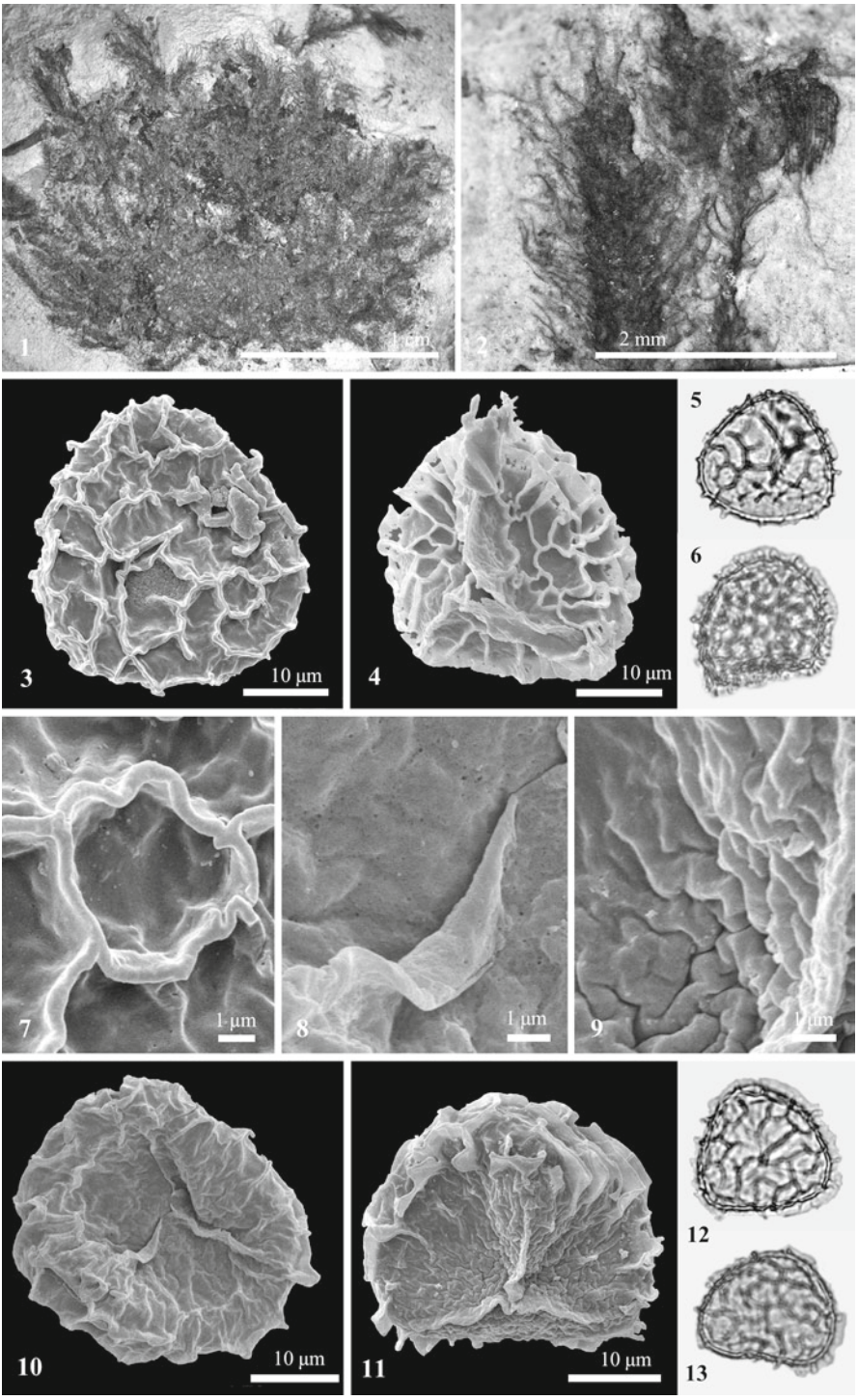



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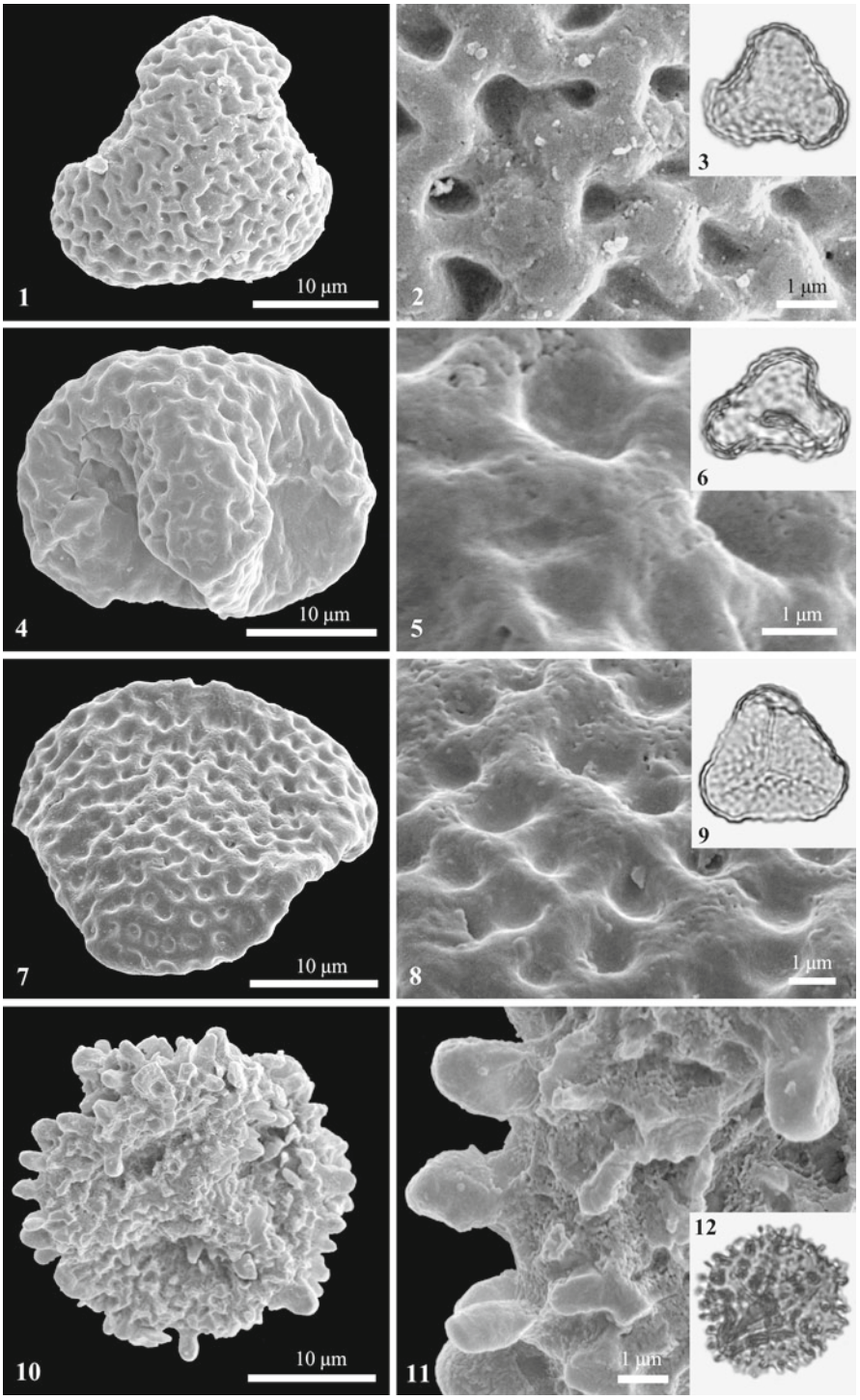



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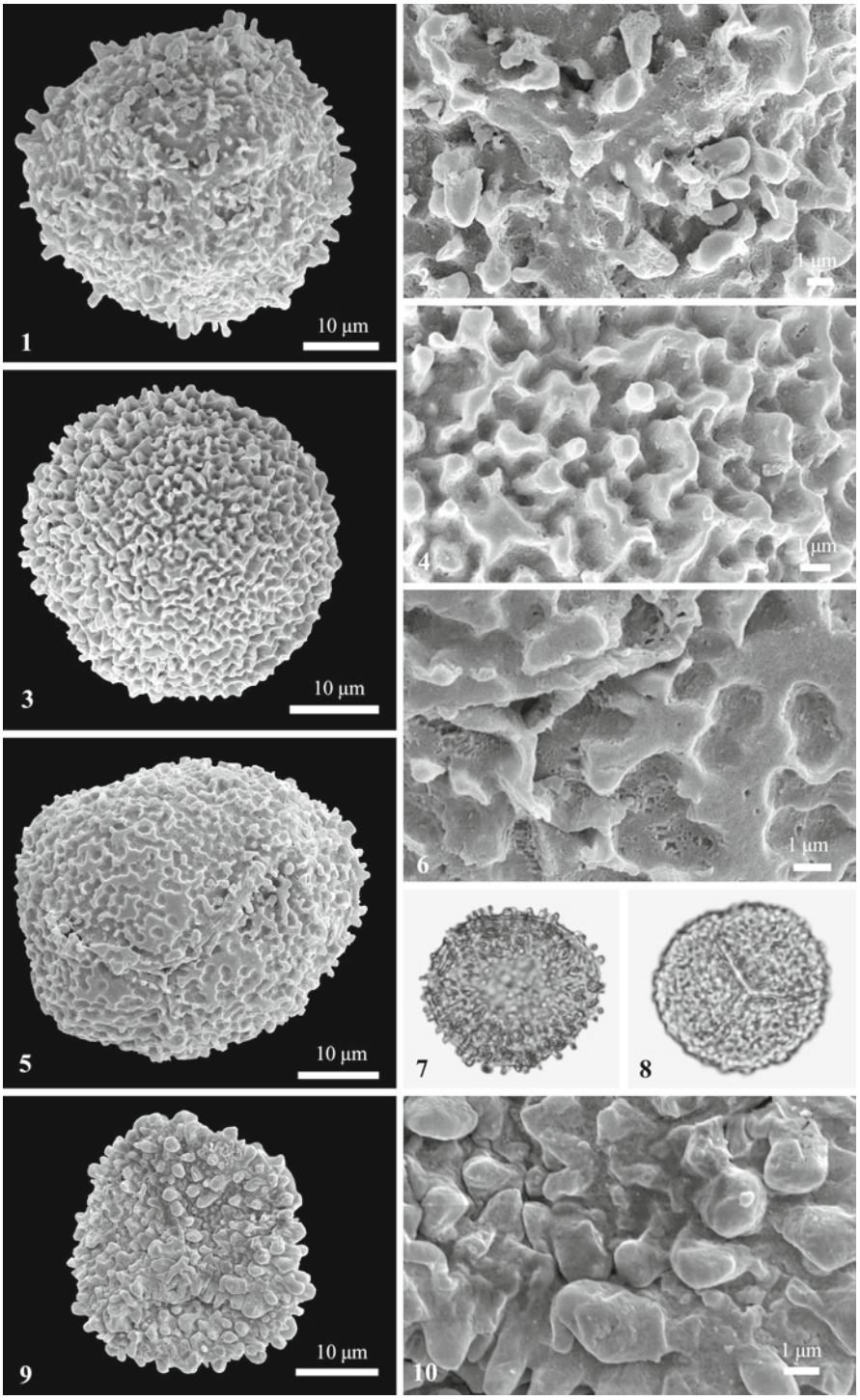



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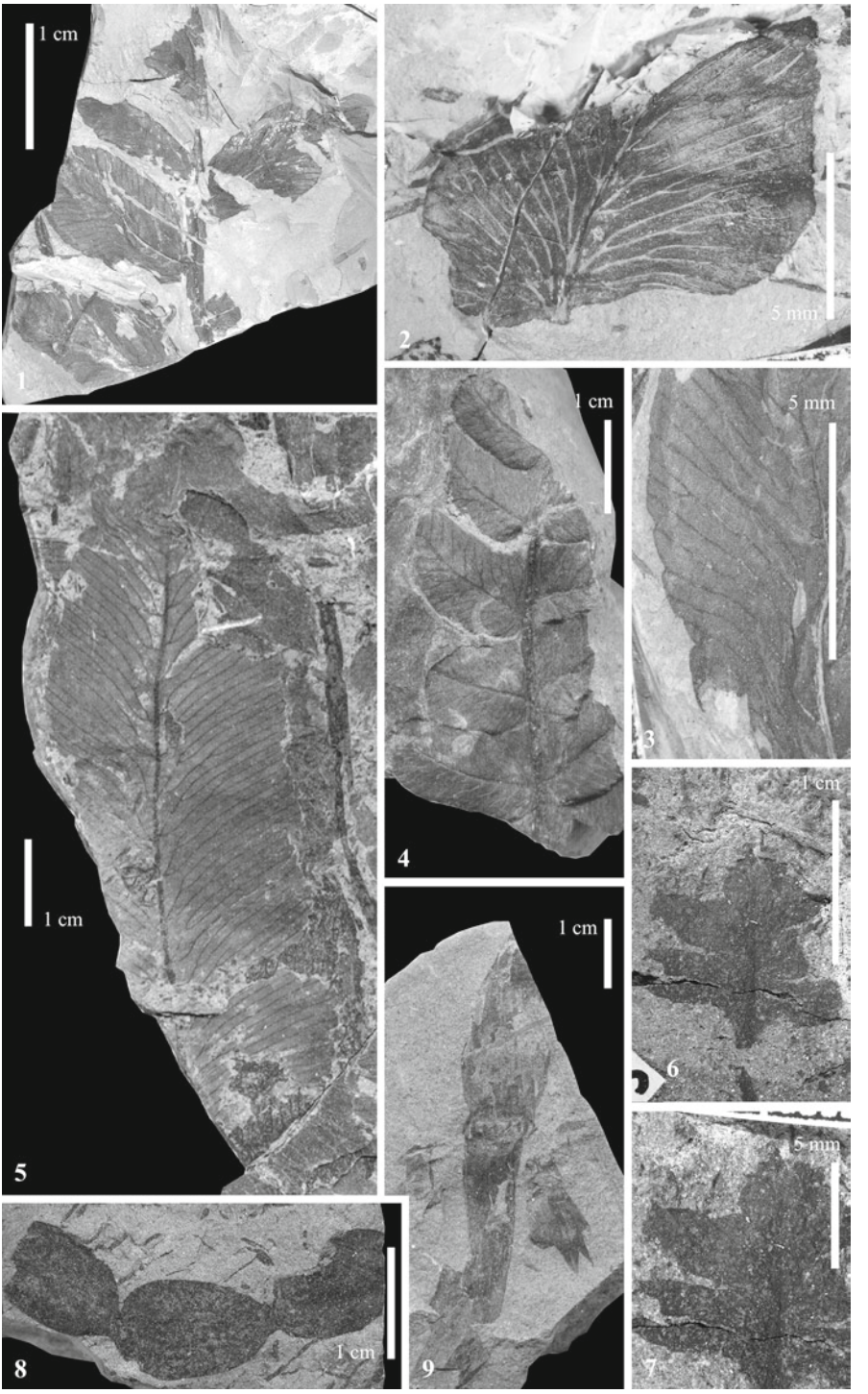



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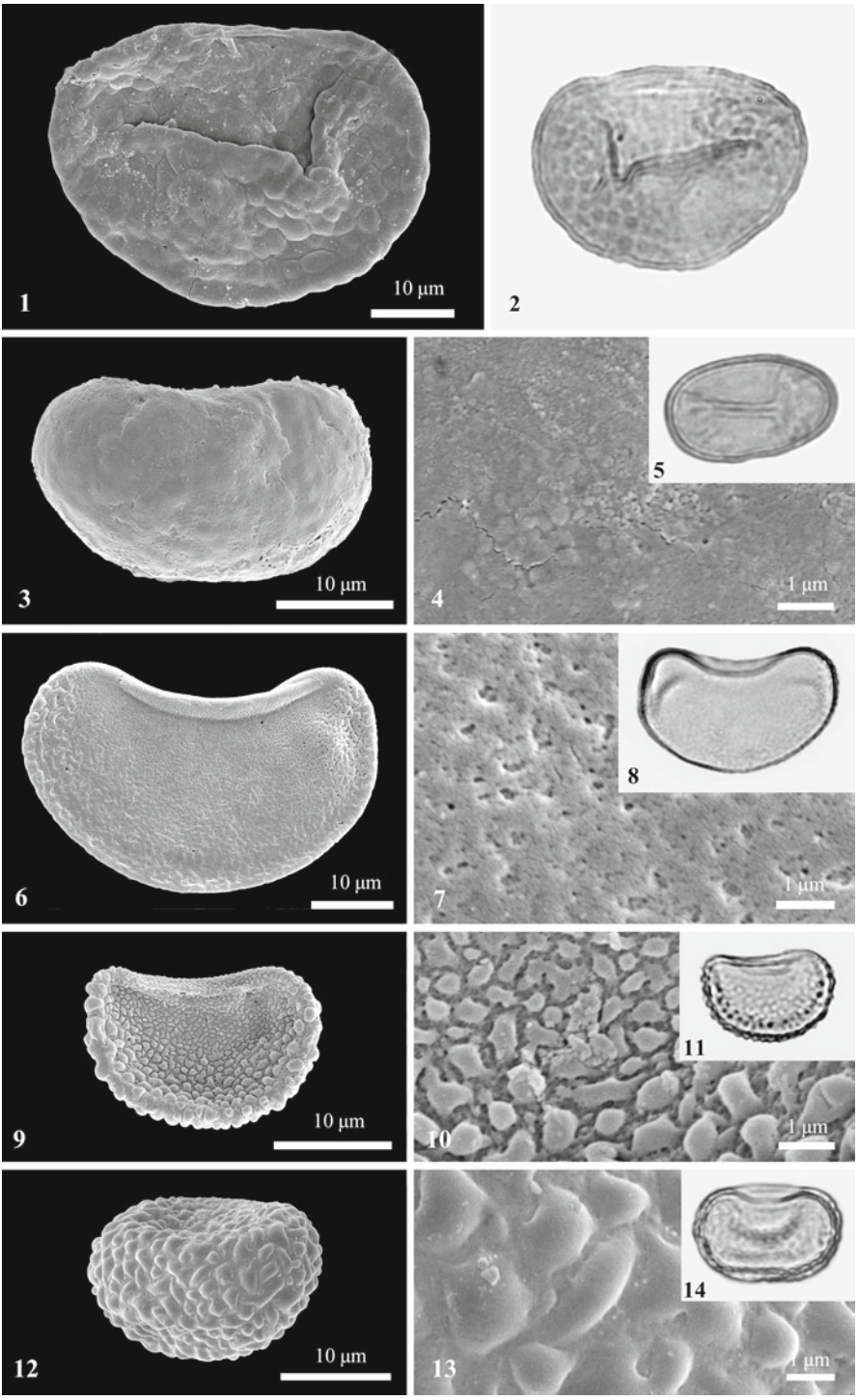

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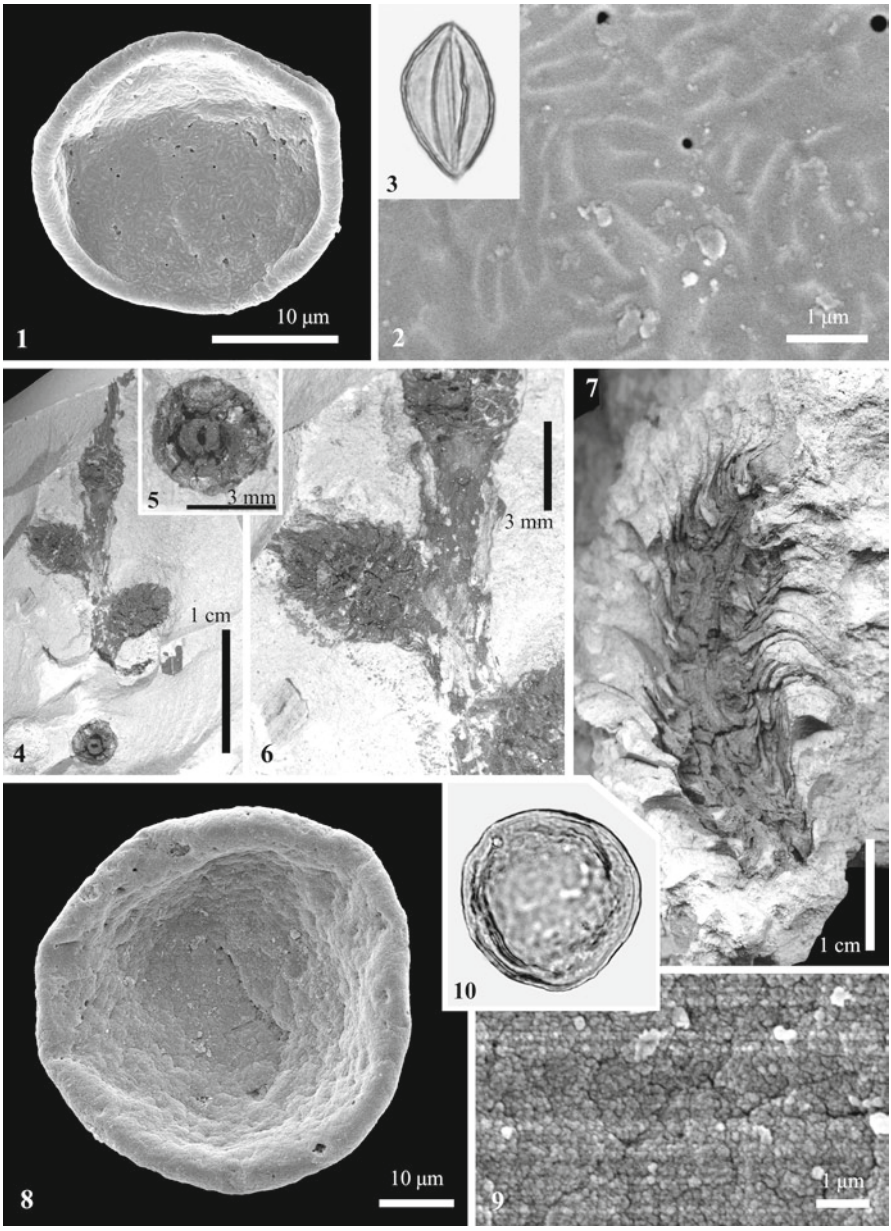



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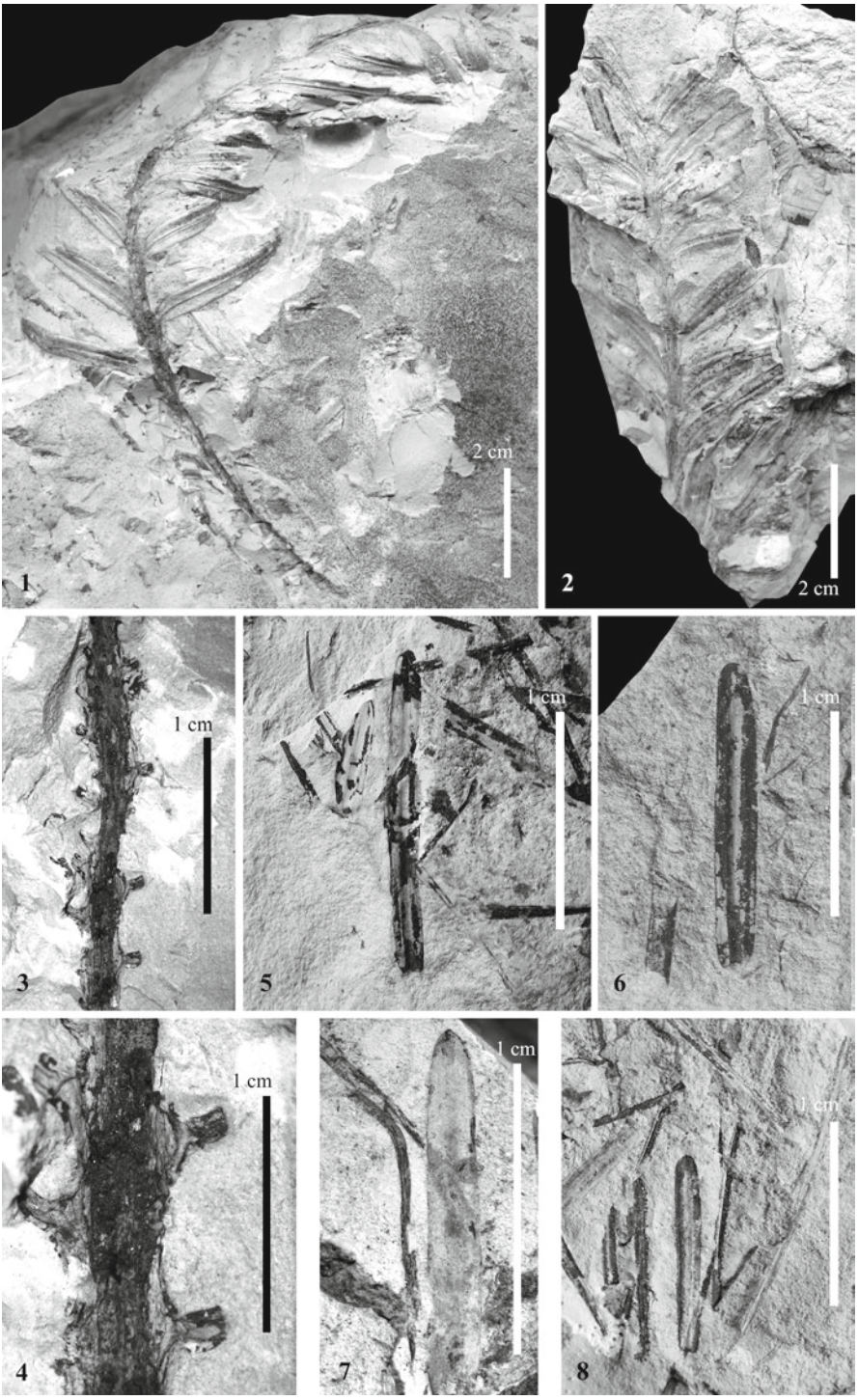



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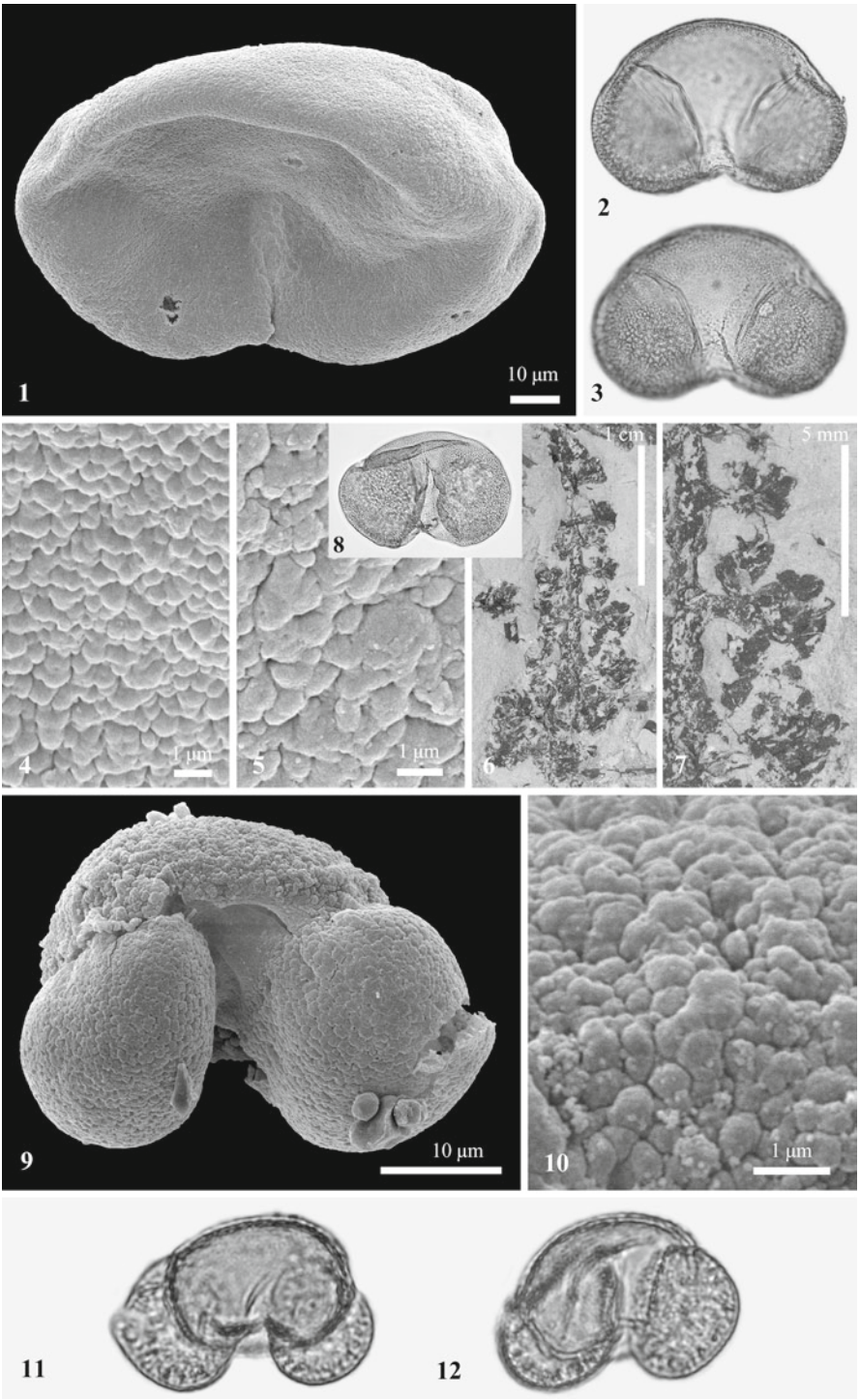



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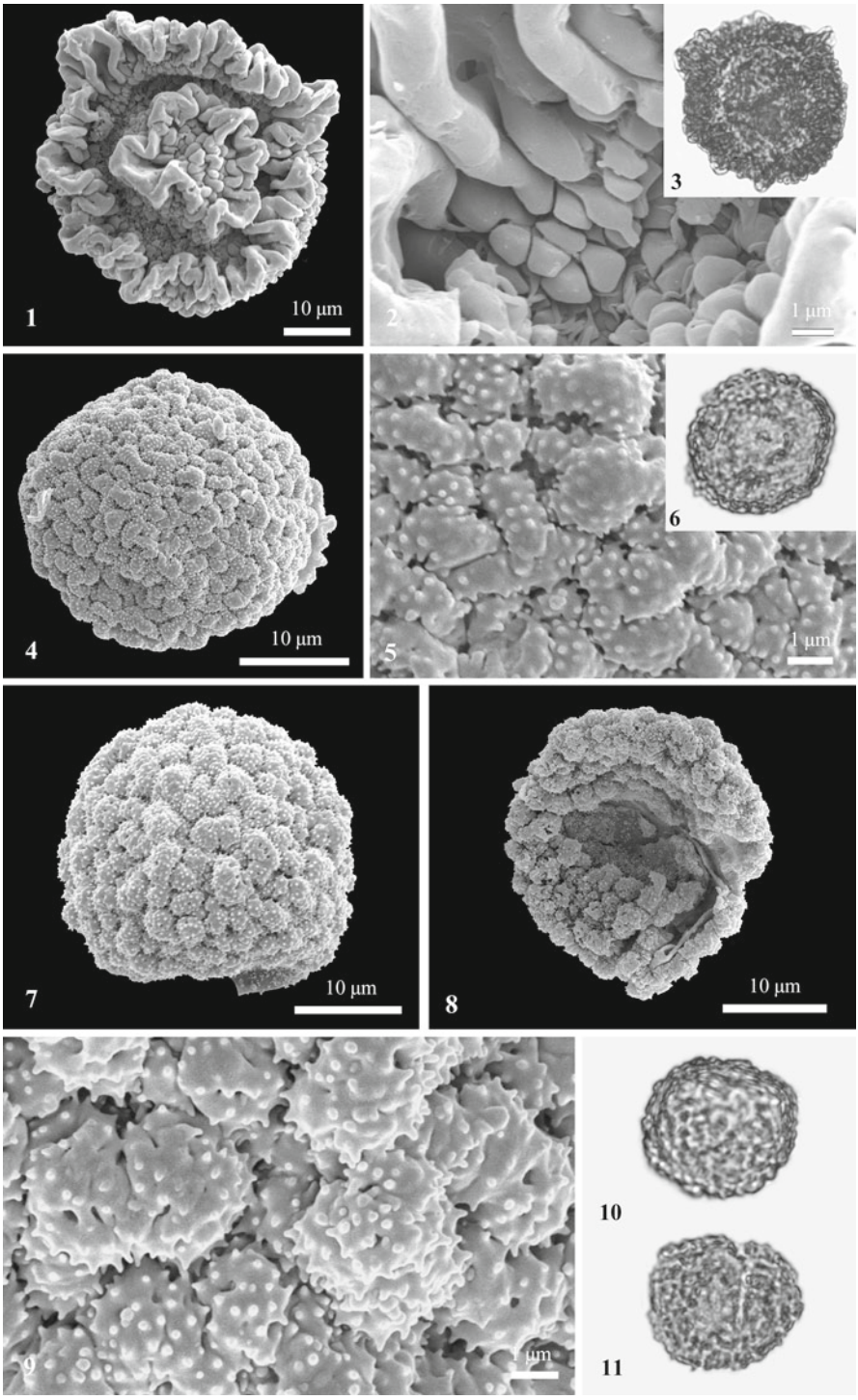



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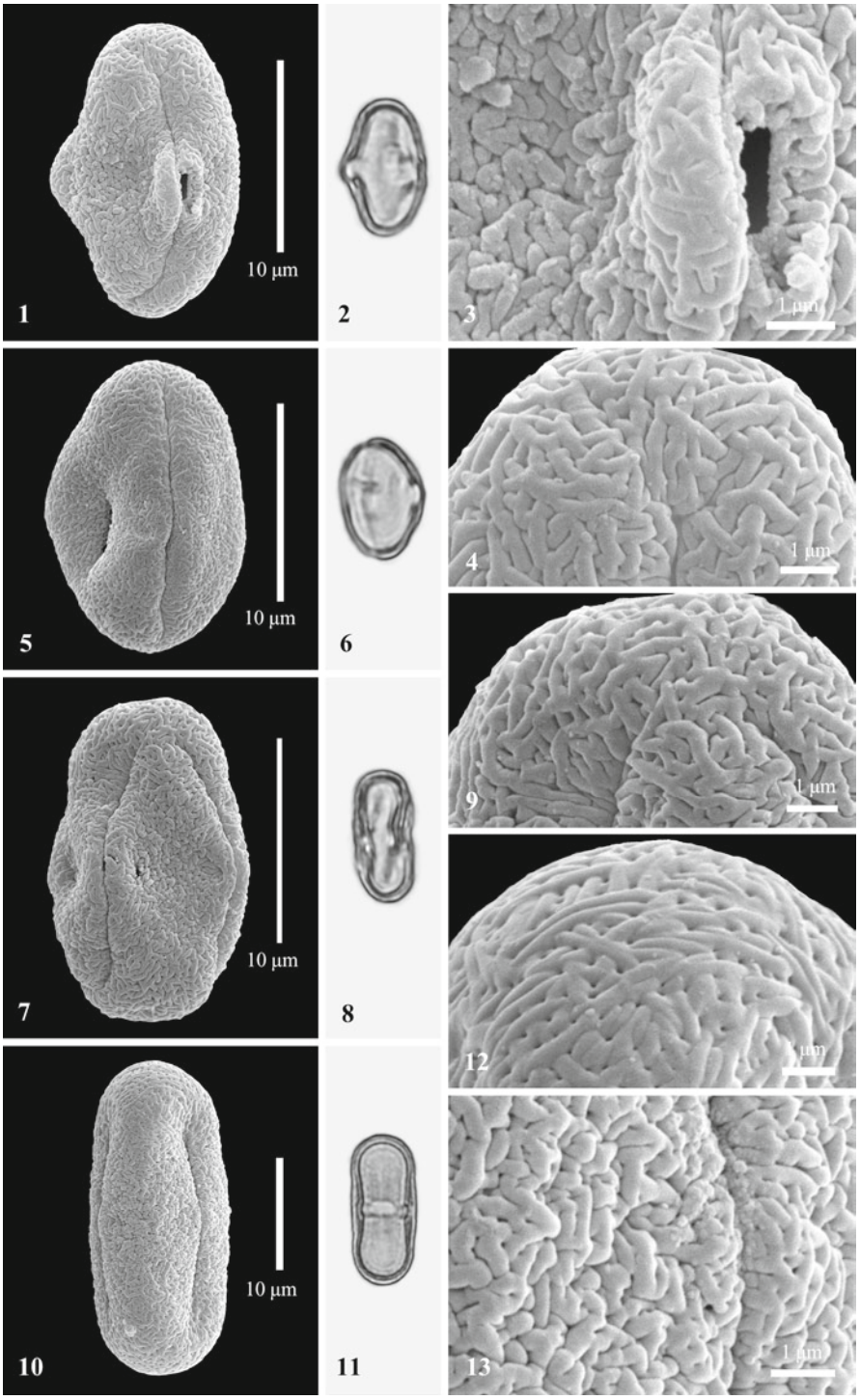



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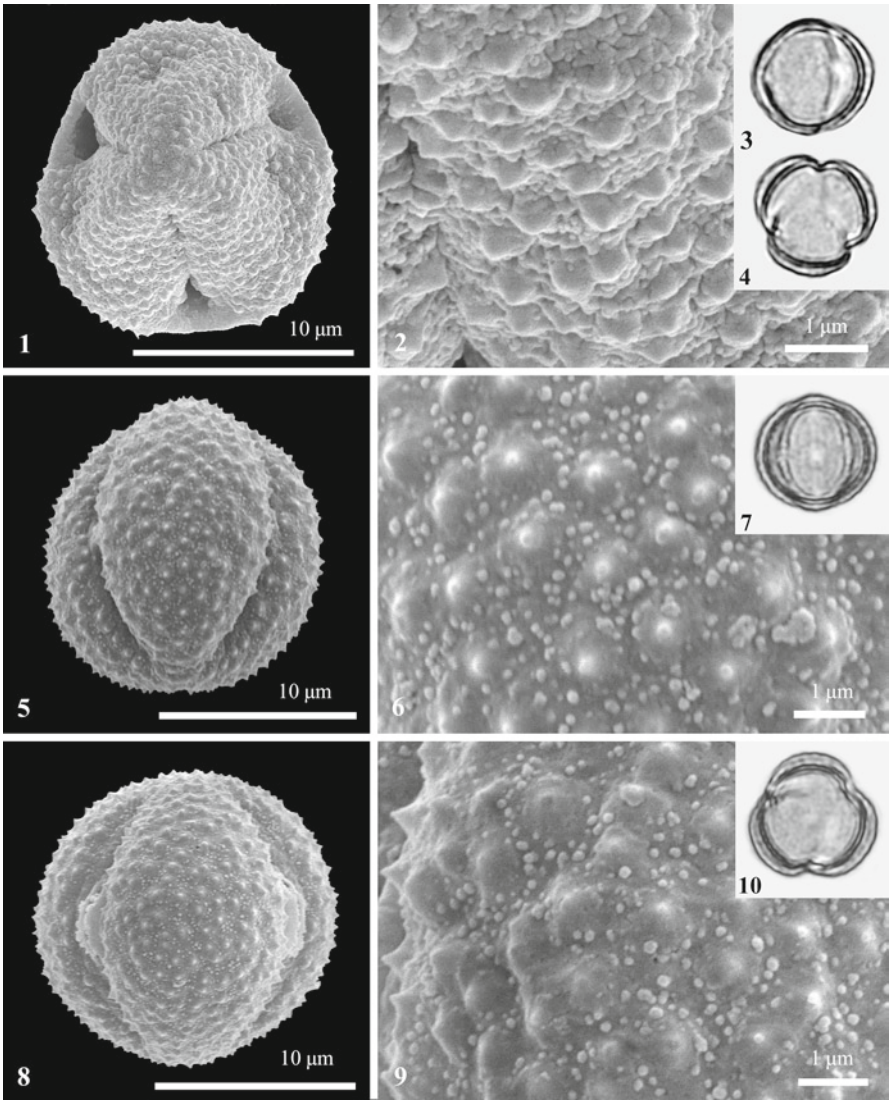



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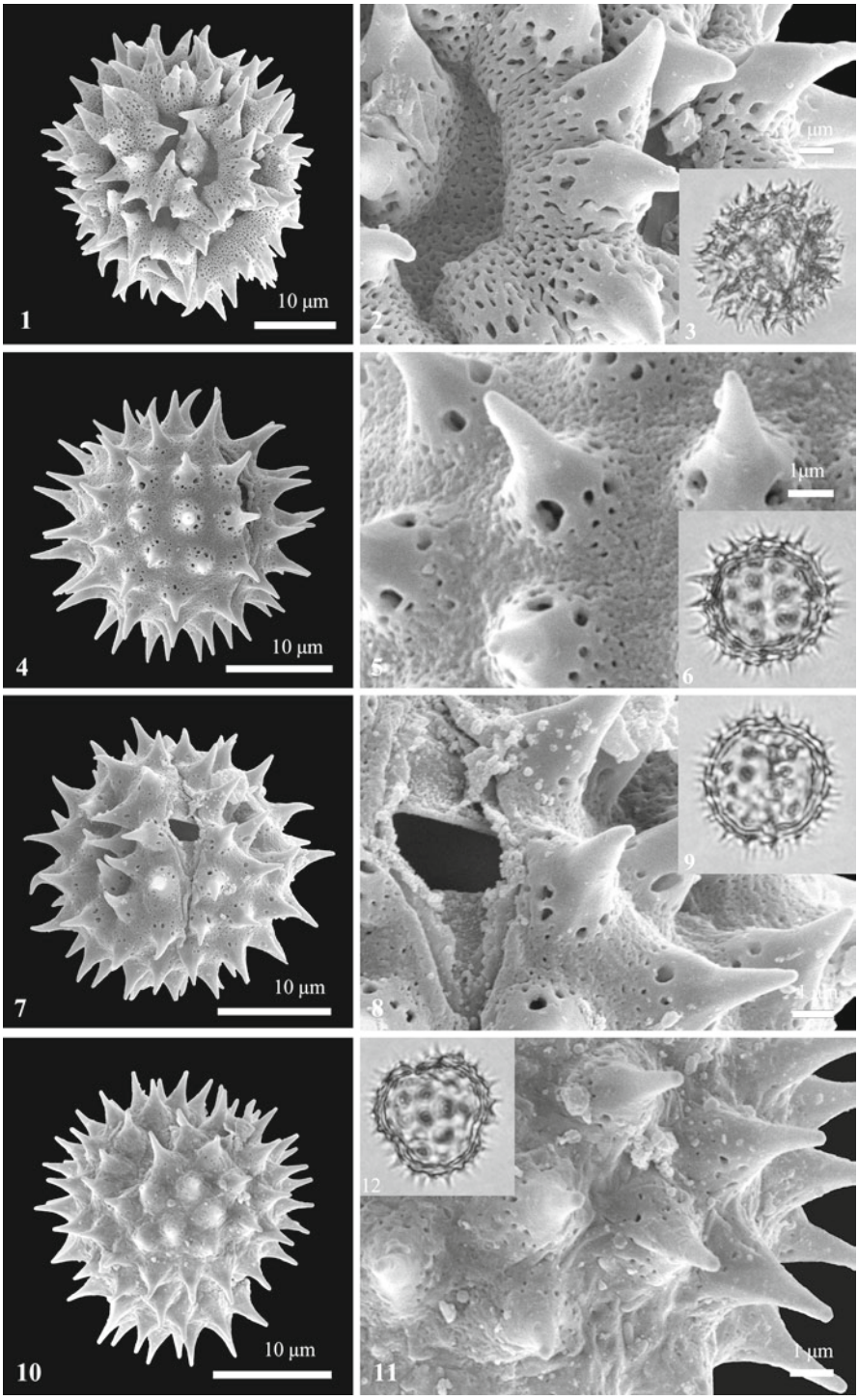



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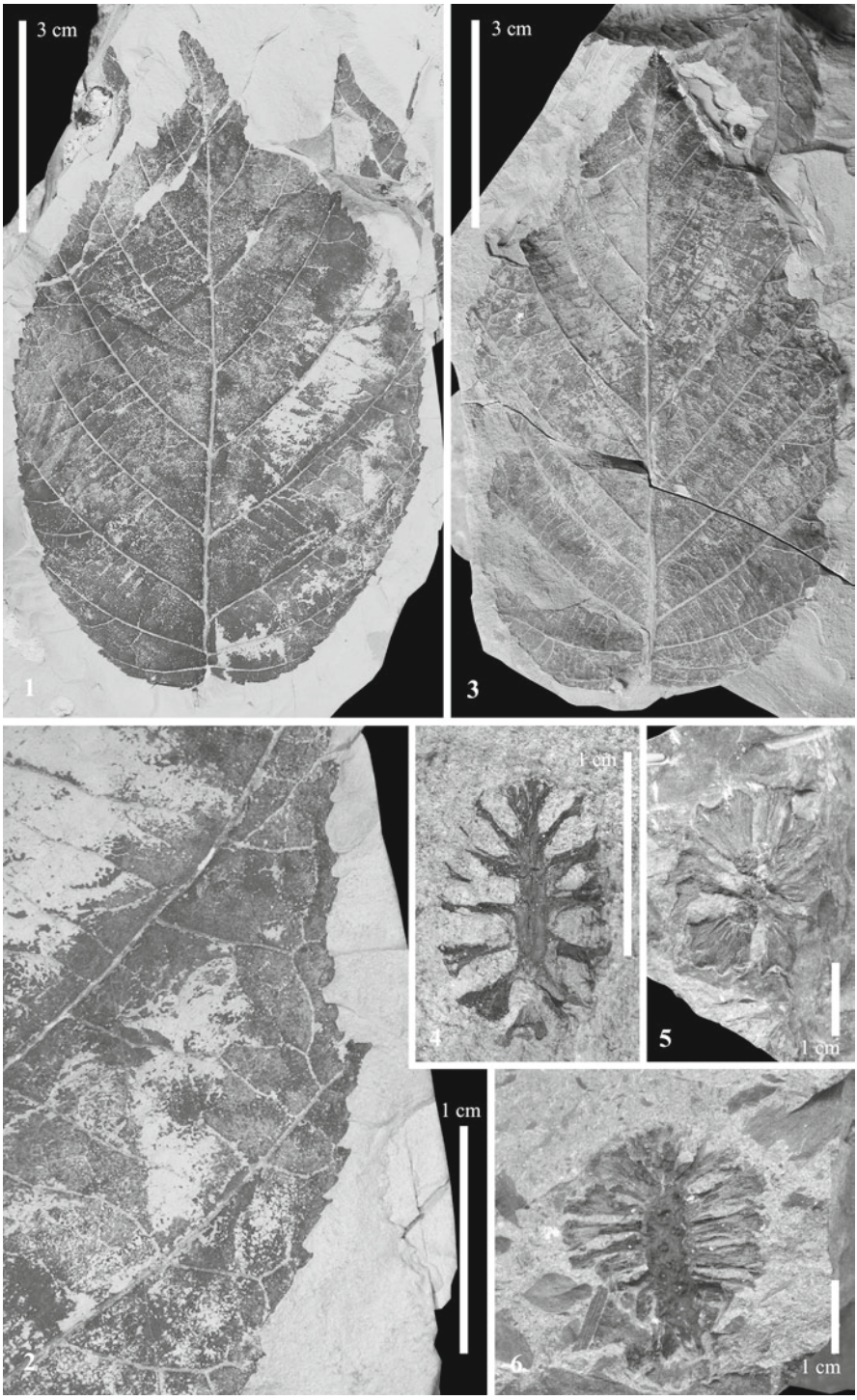



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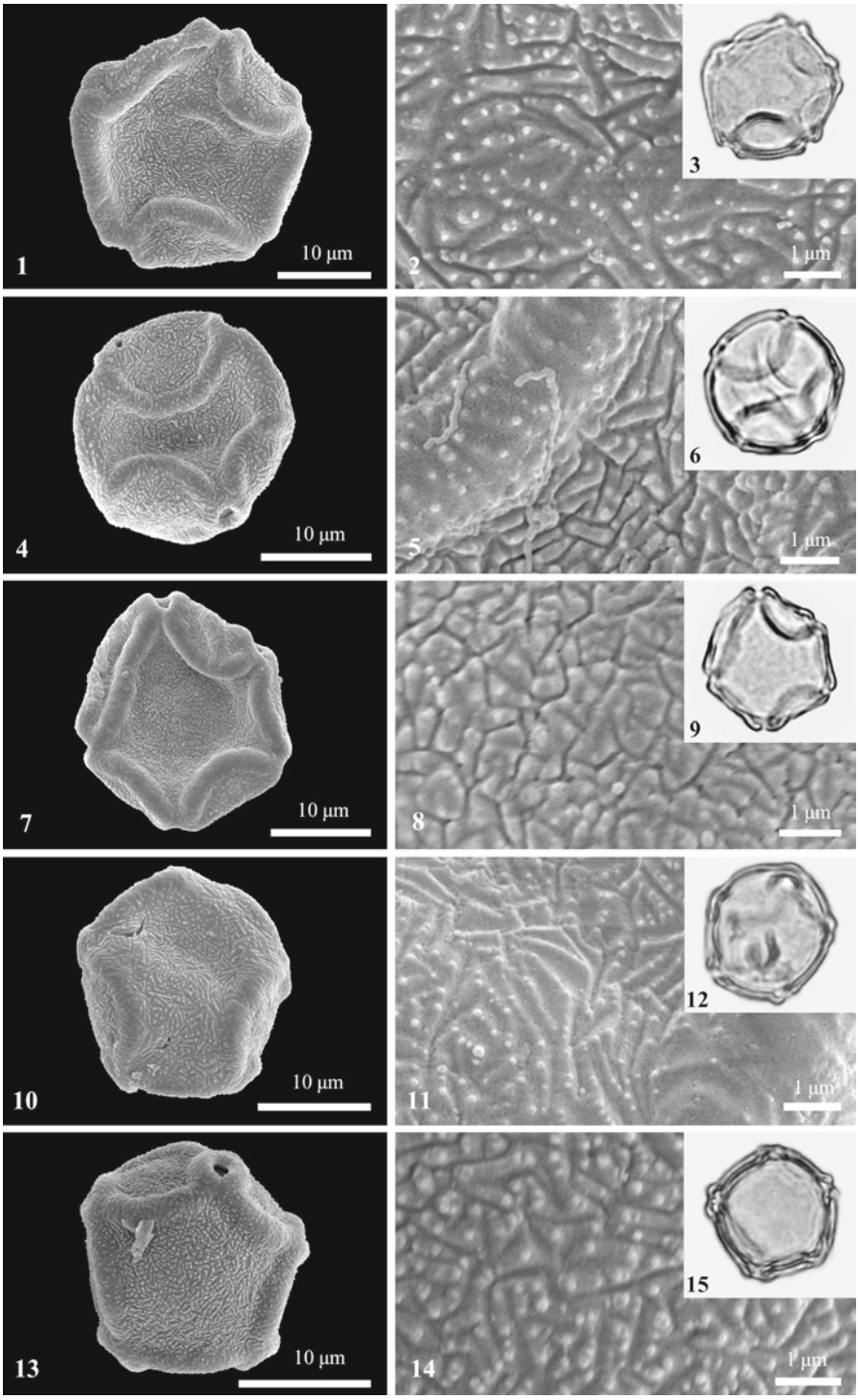

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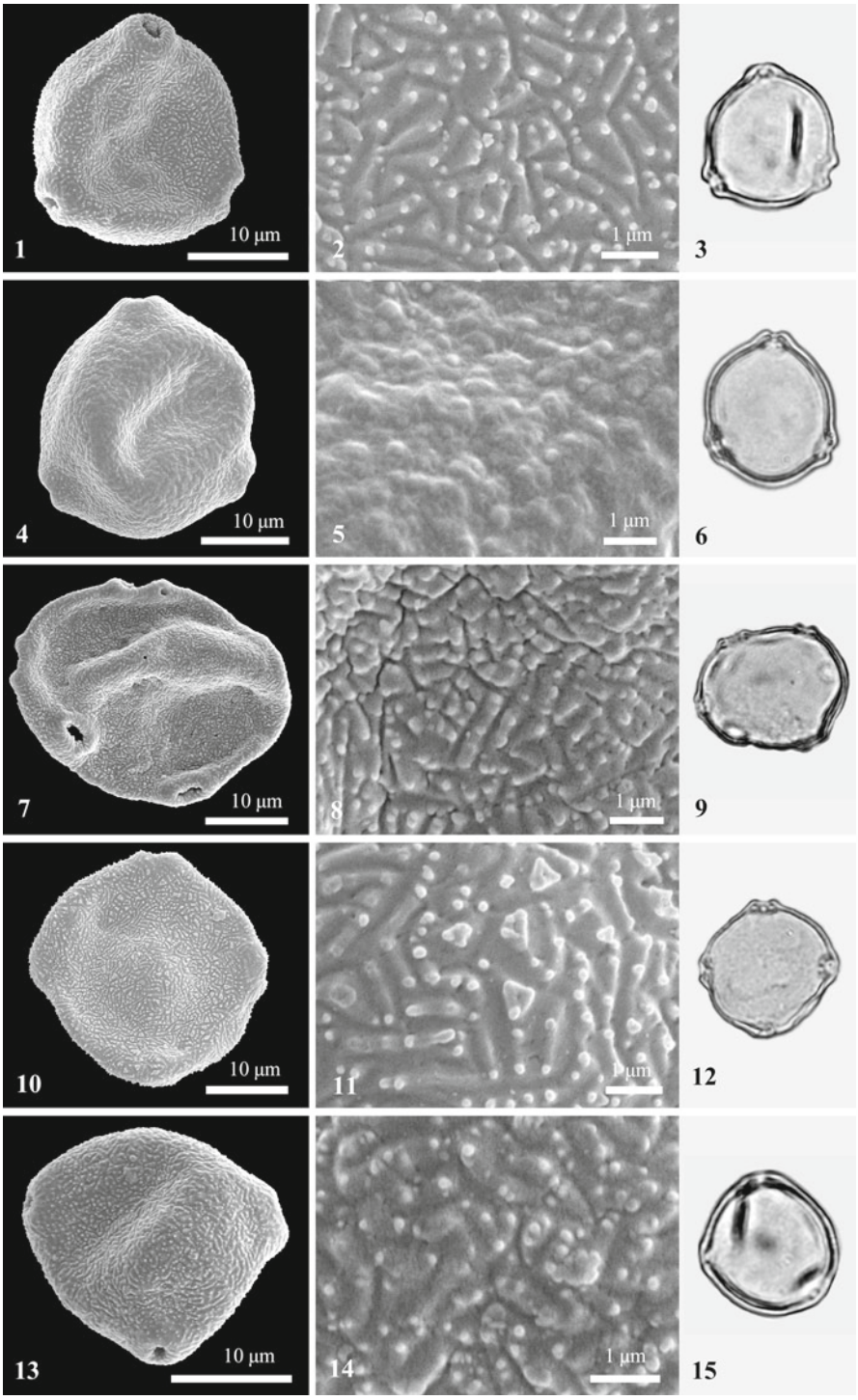

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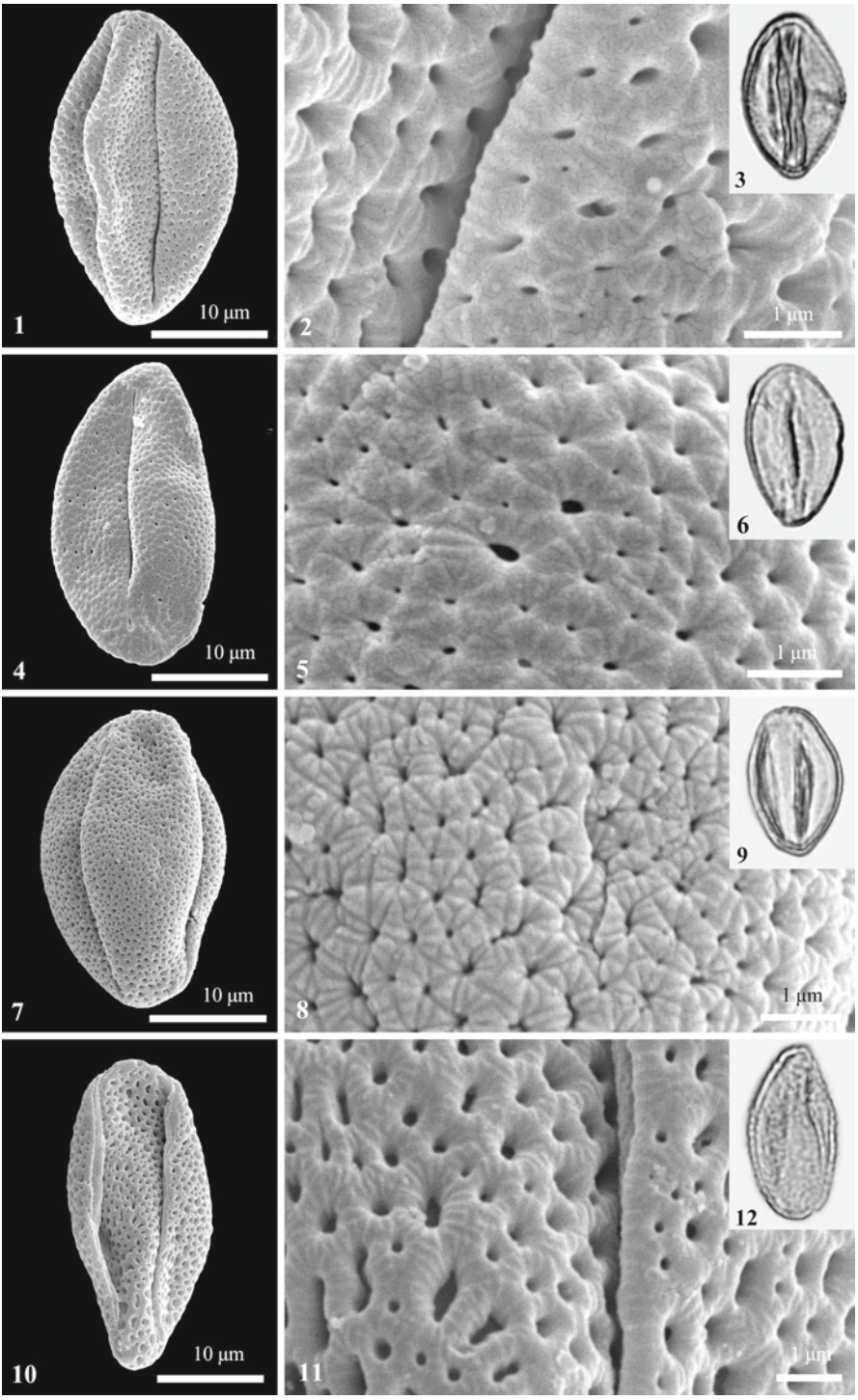



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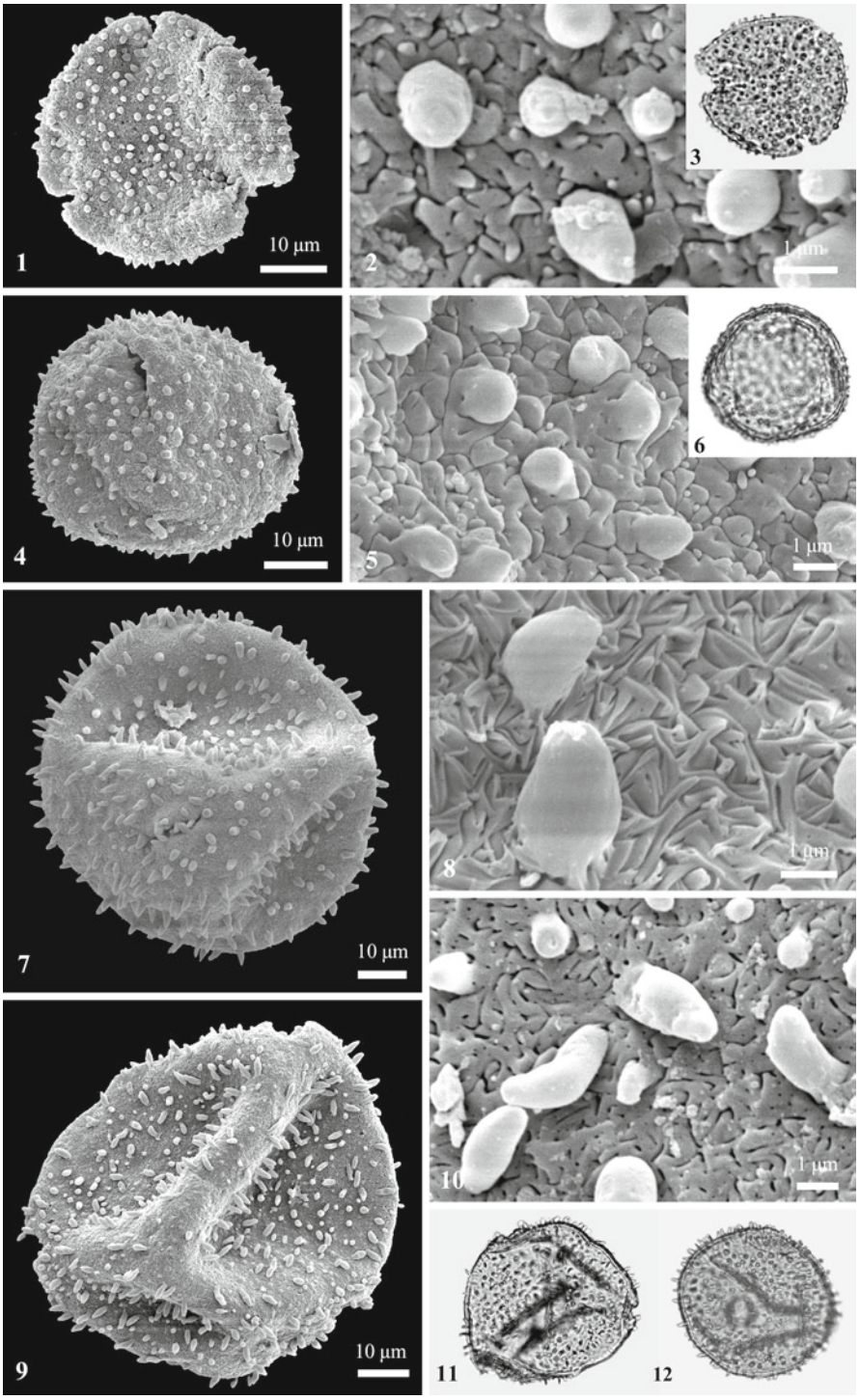



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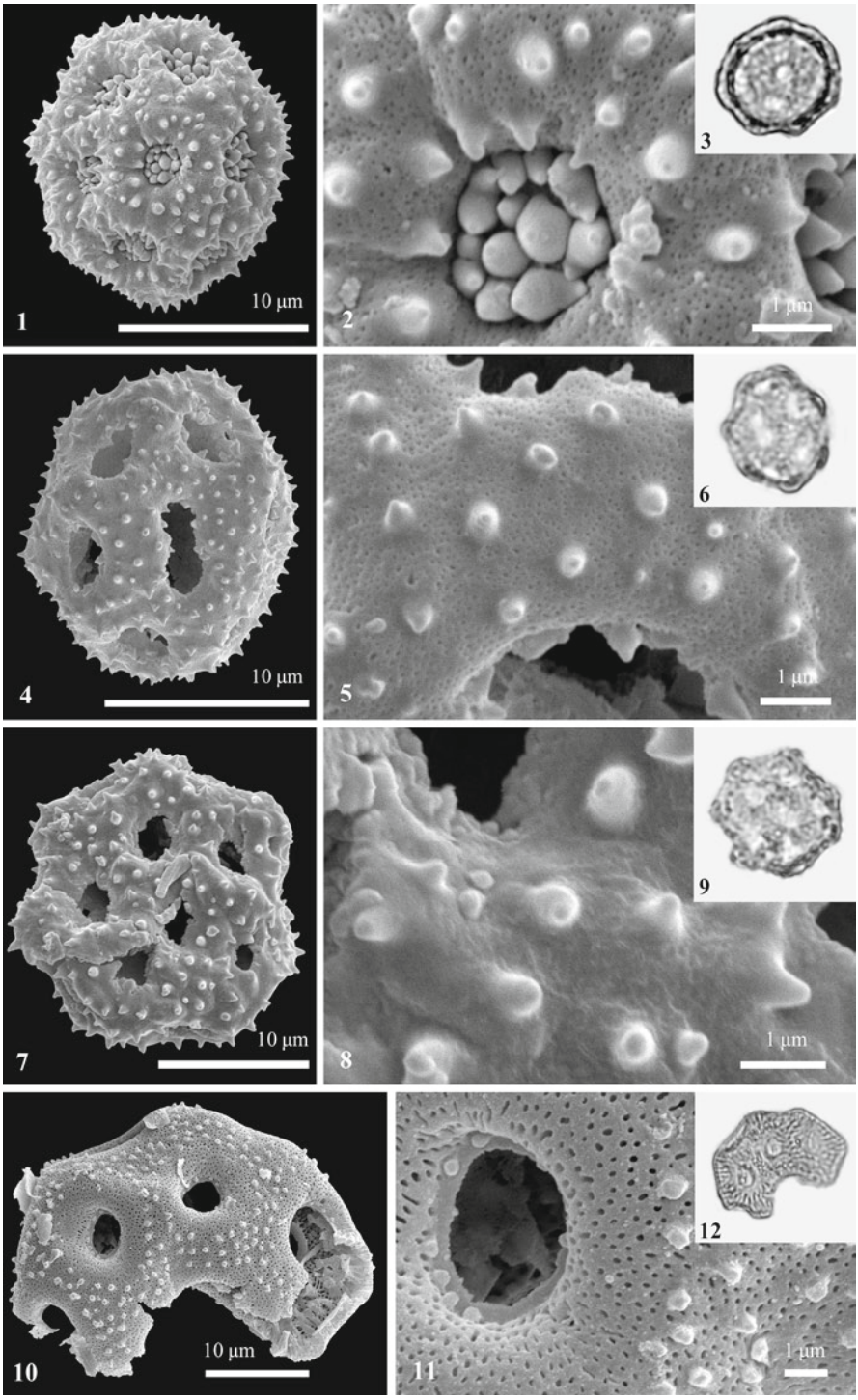



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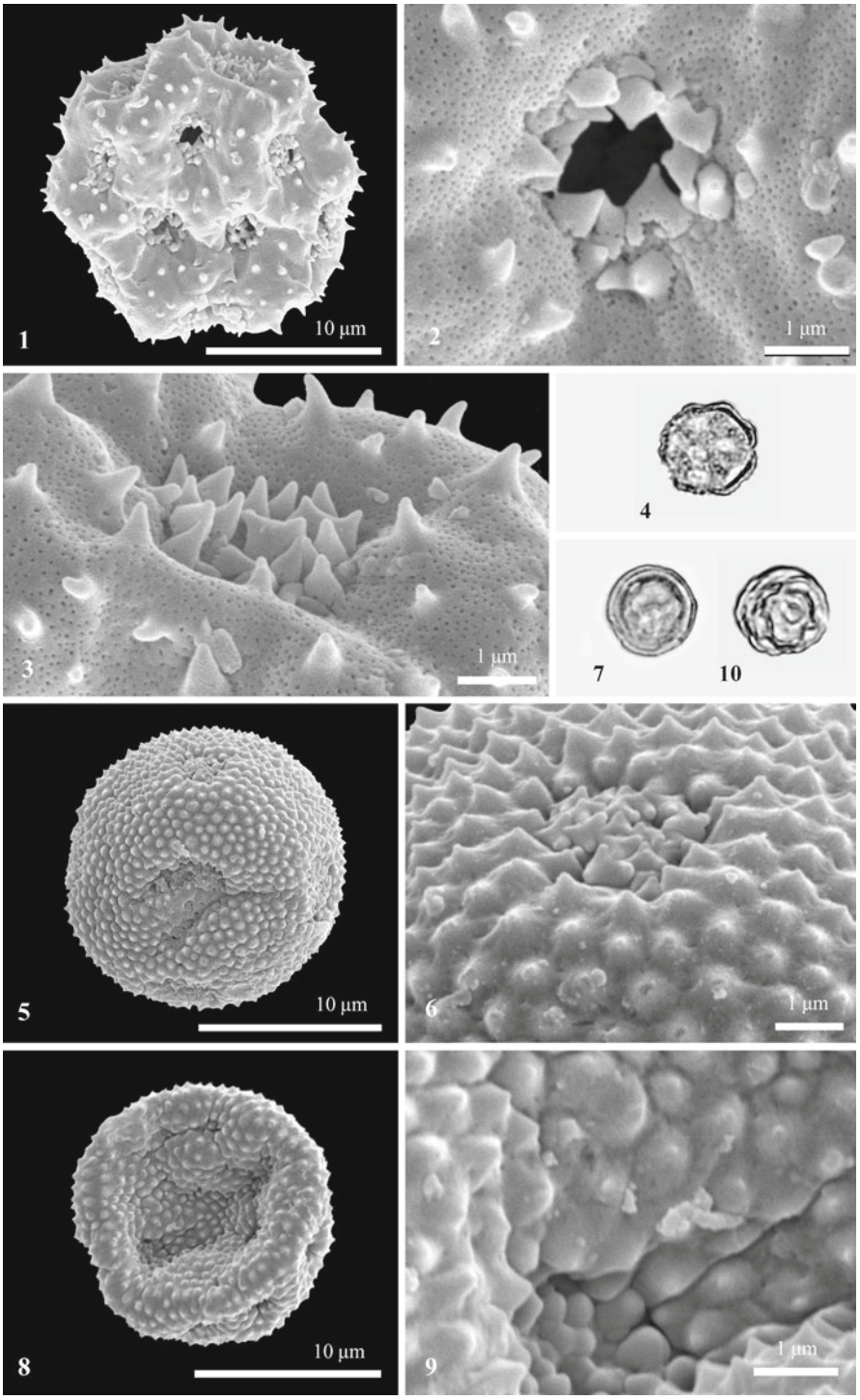



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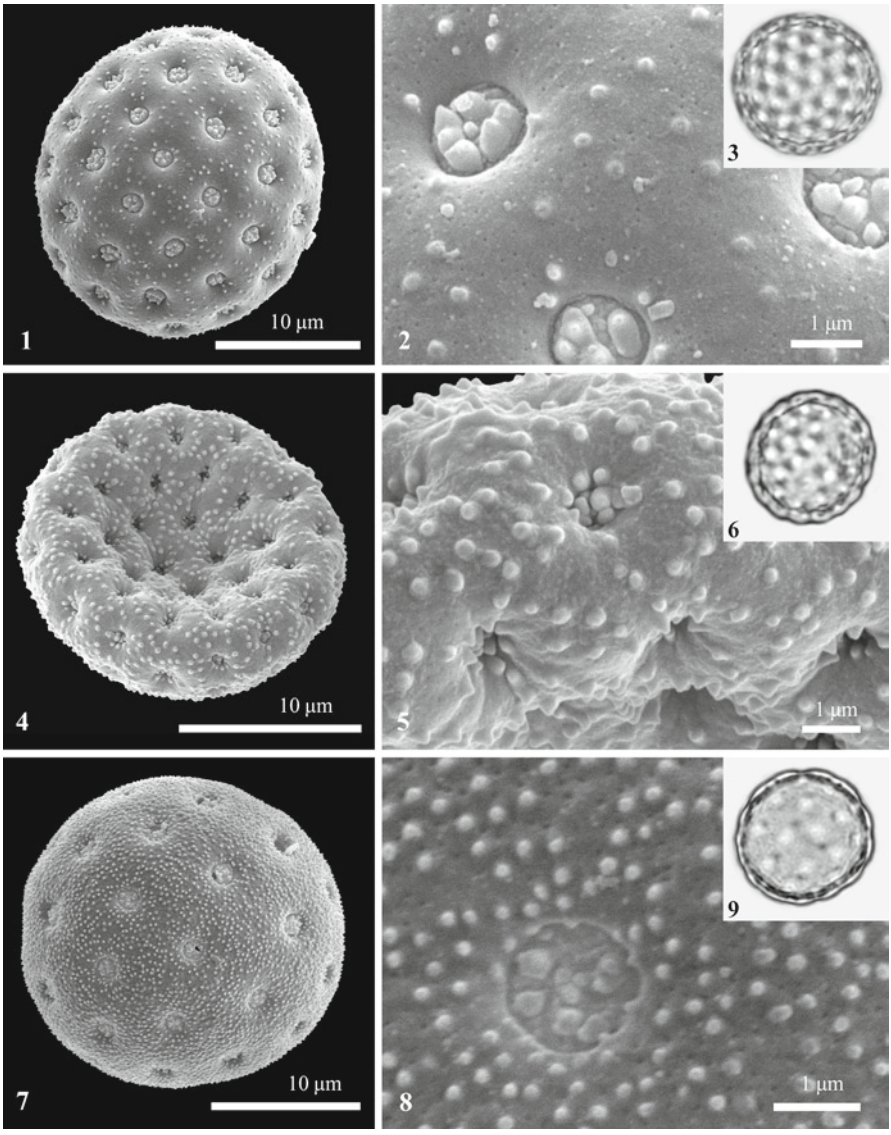



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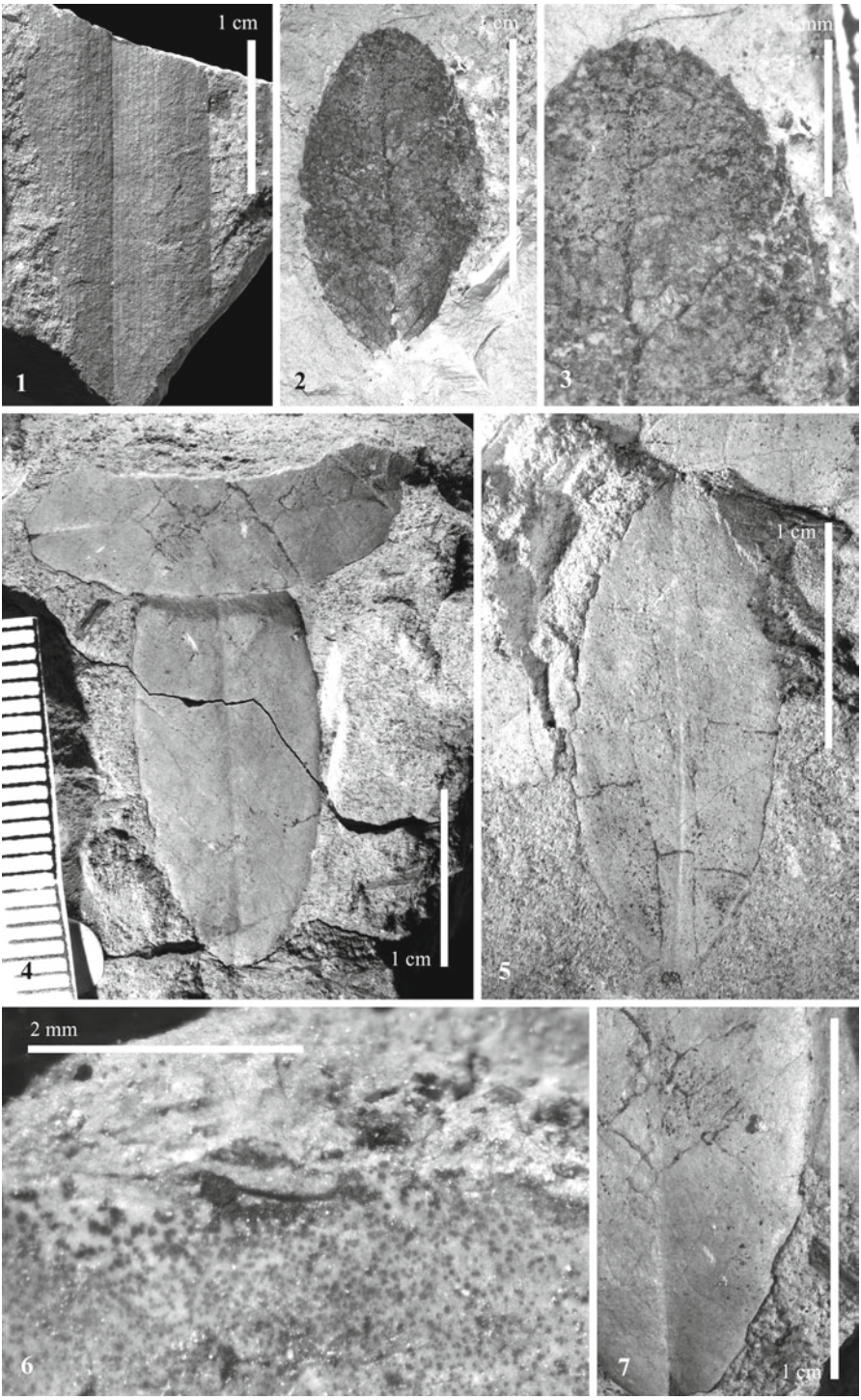



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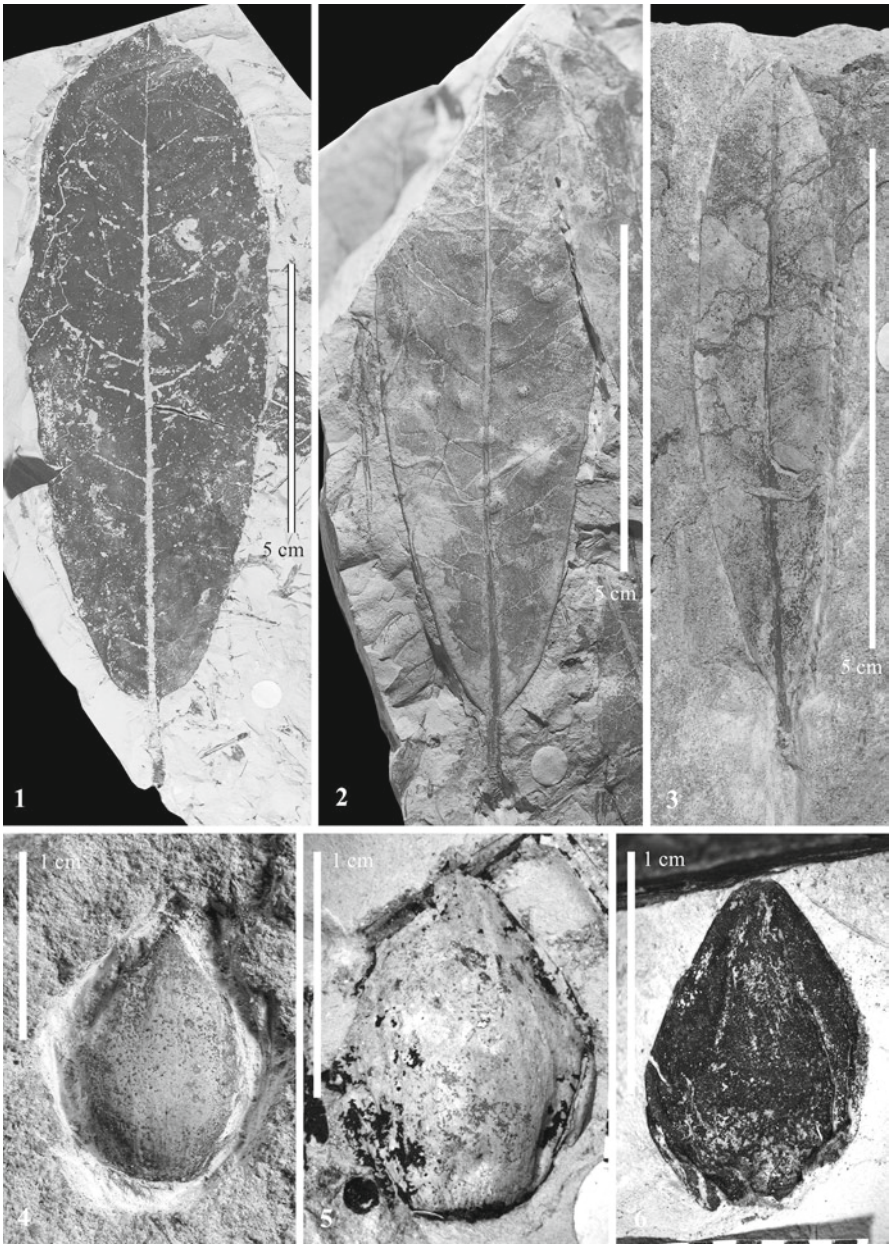



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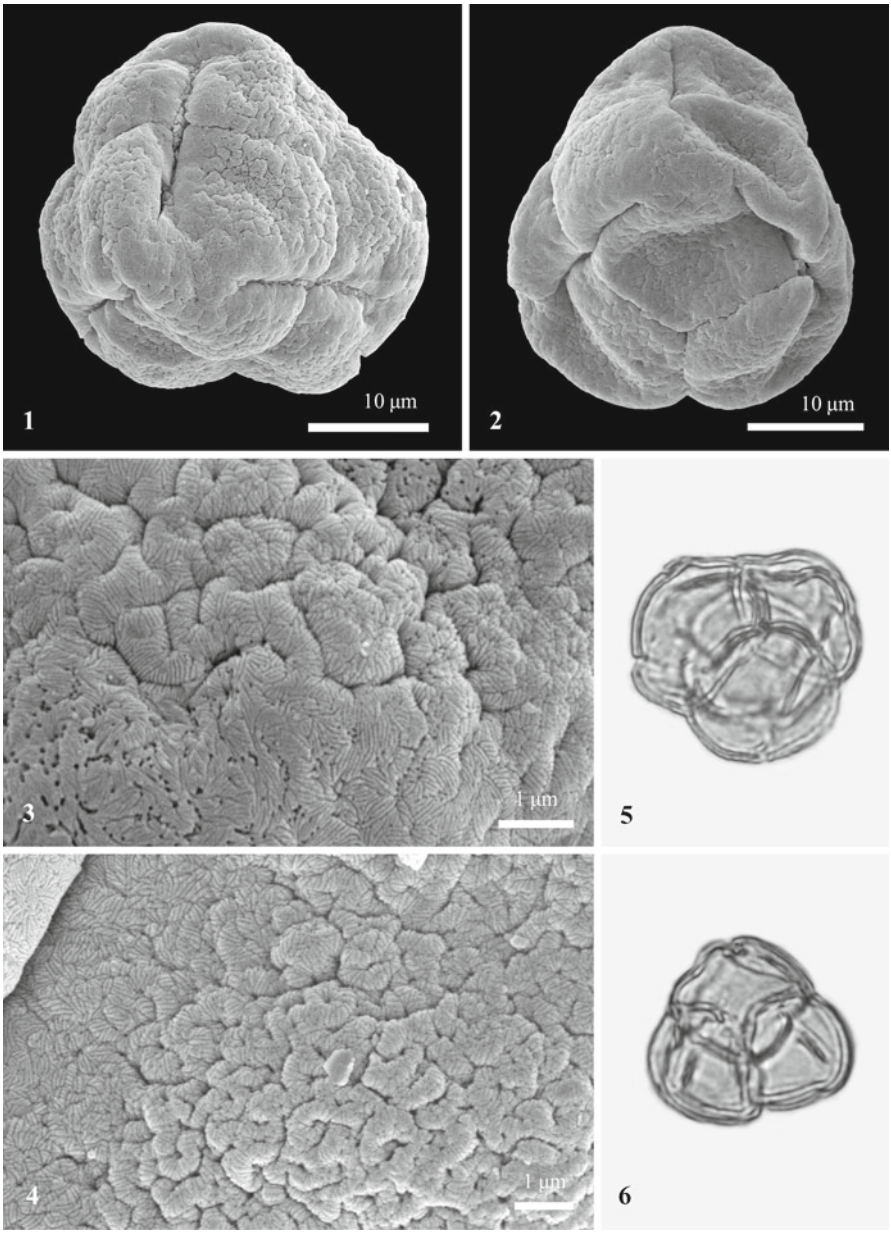



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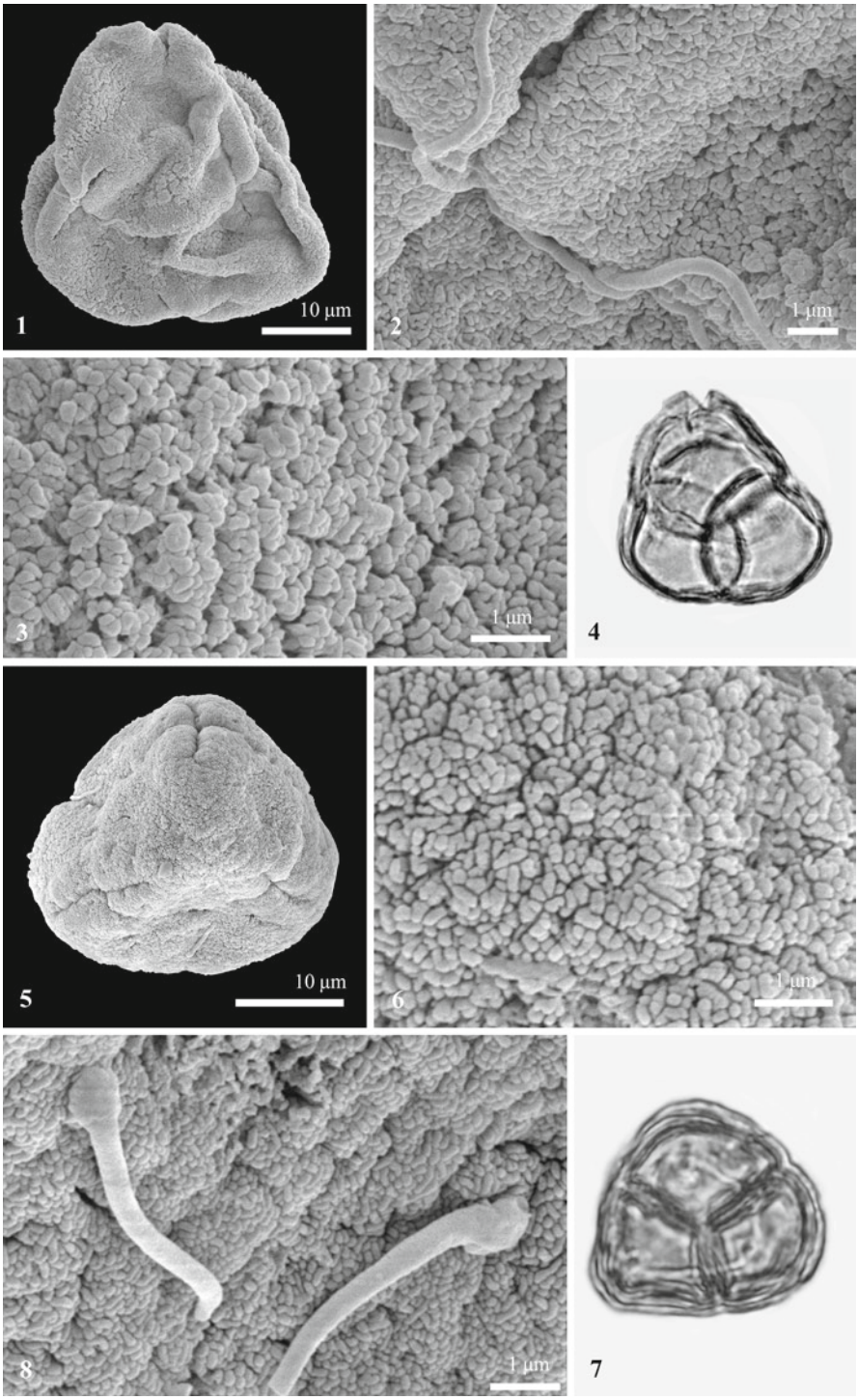



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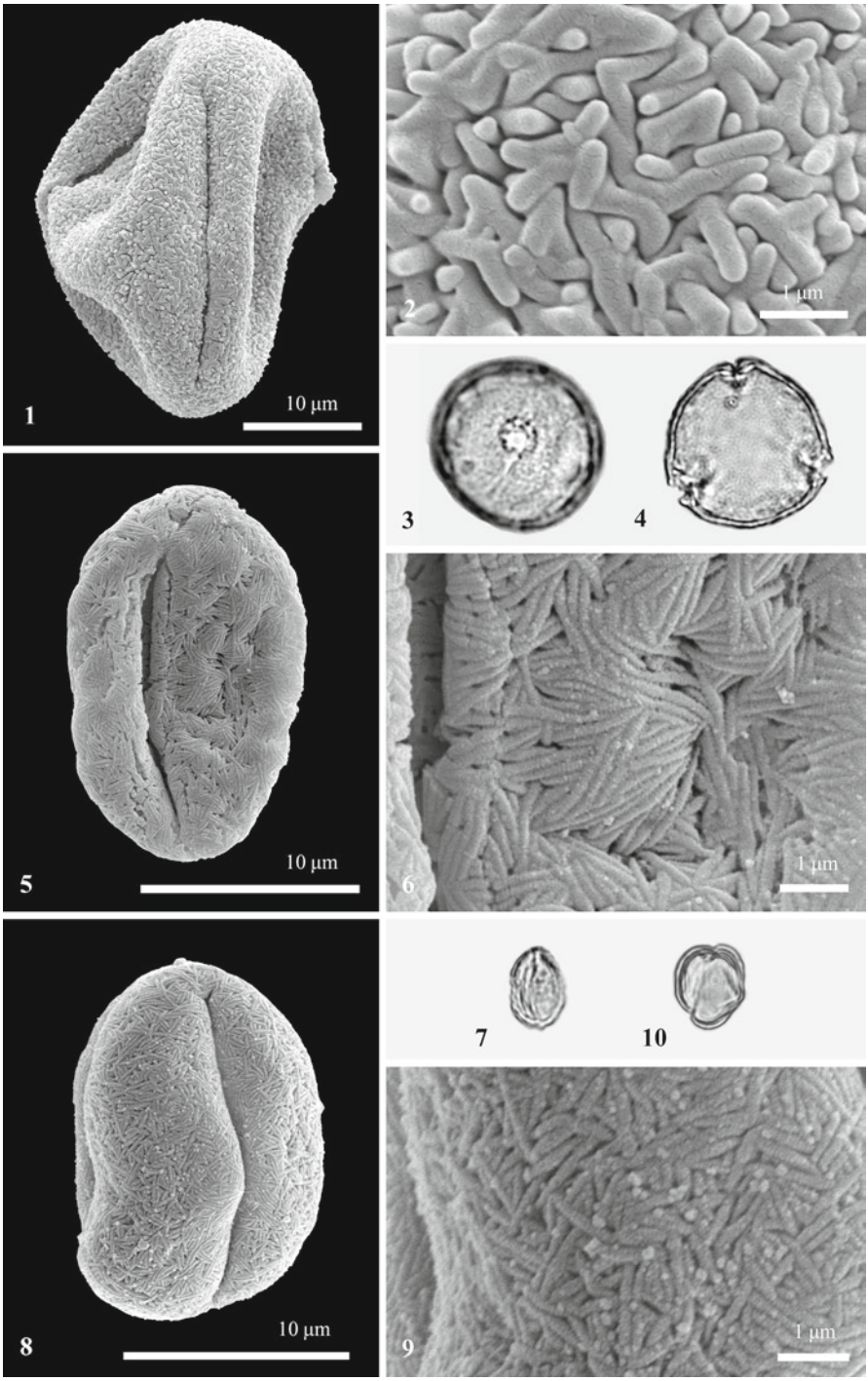



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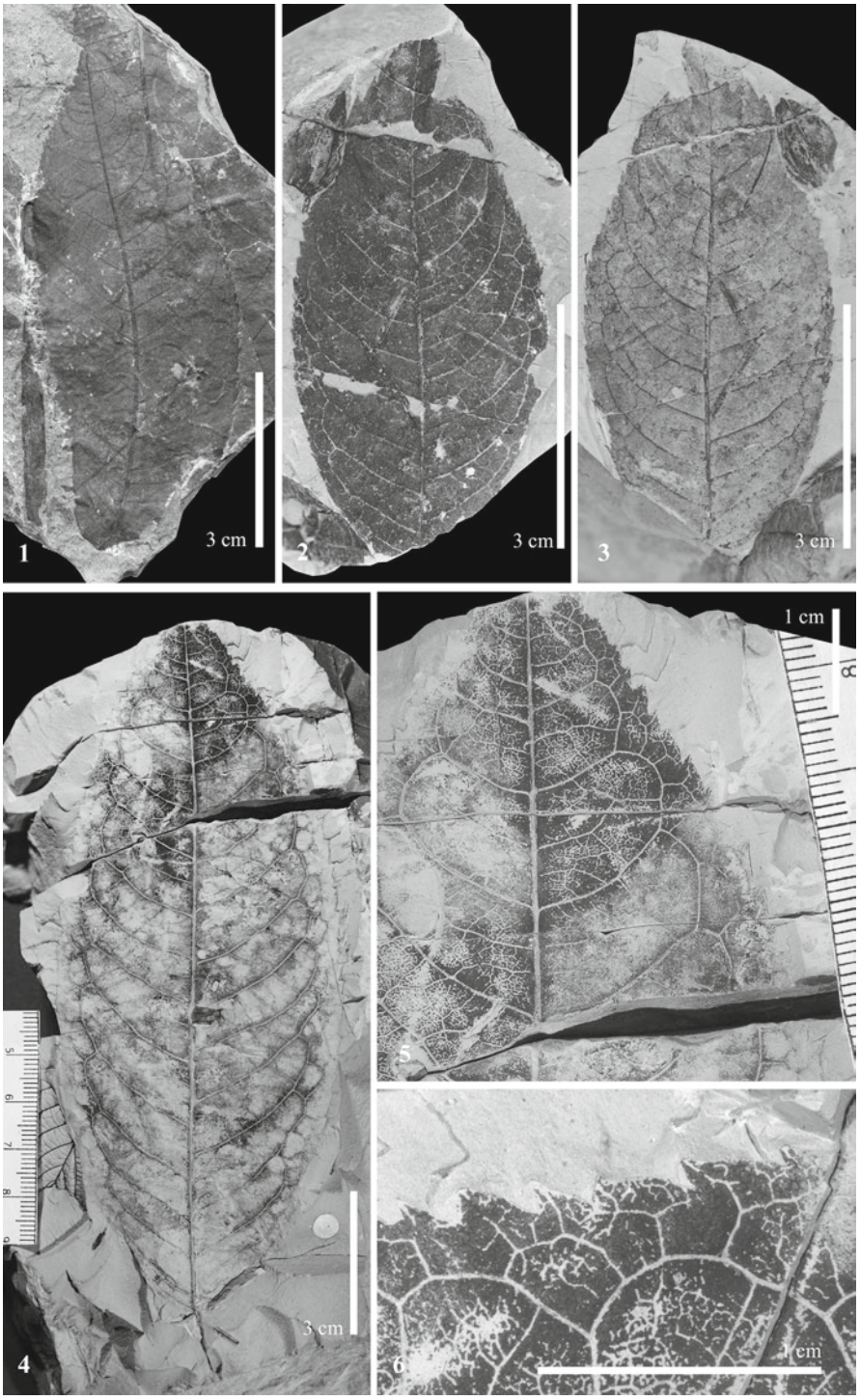



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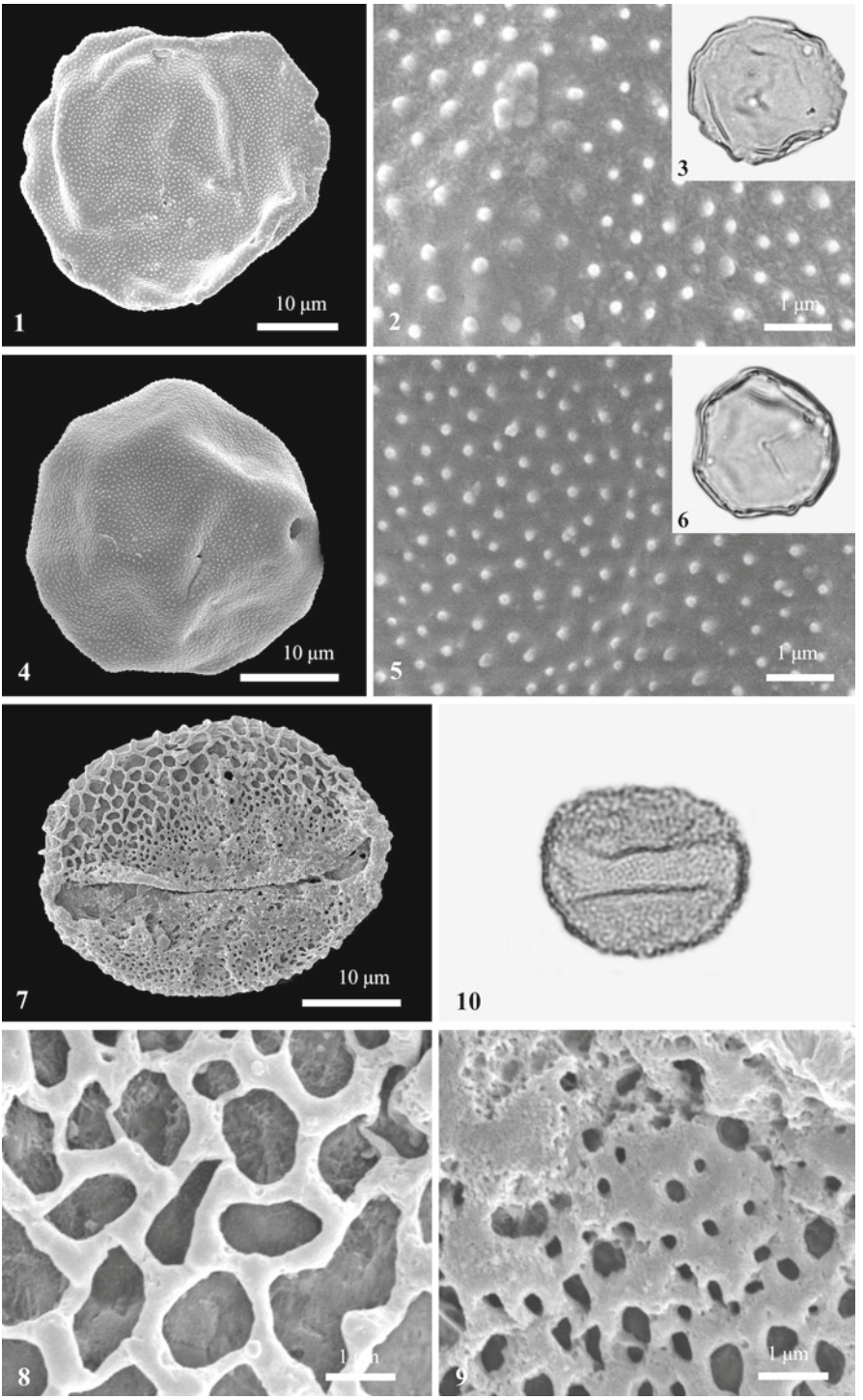



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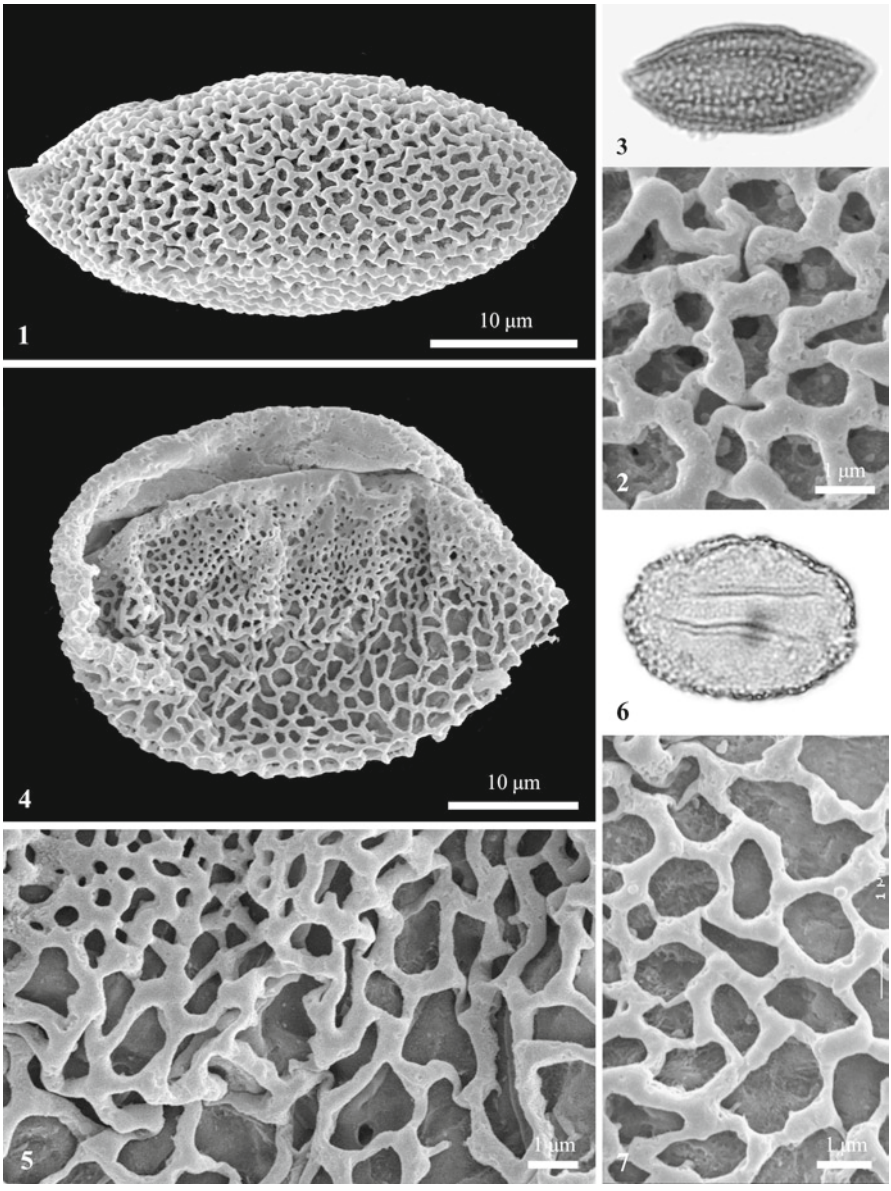



**Plate 6.30**

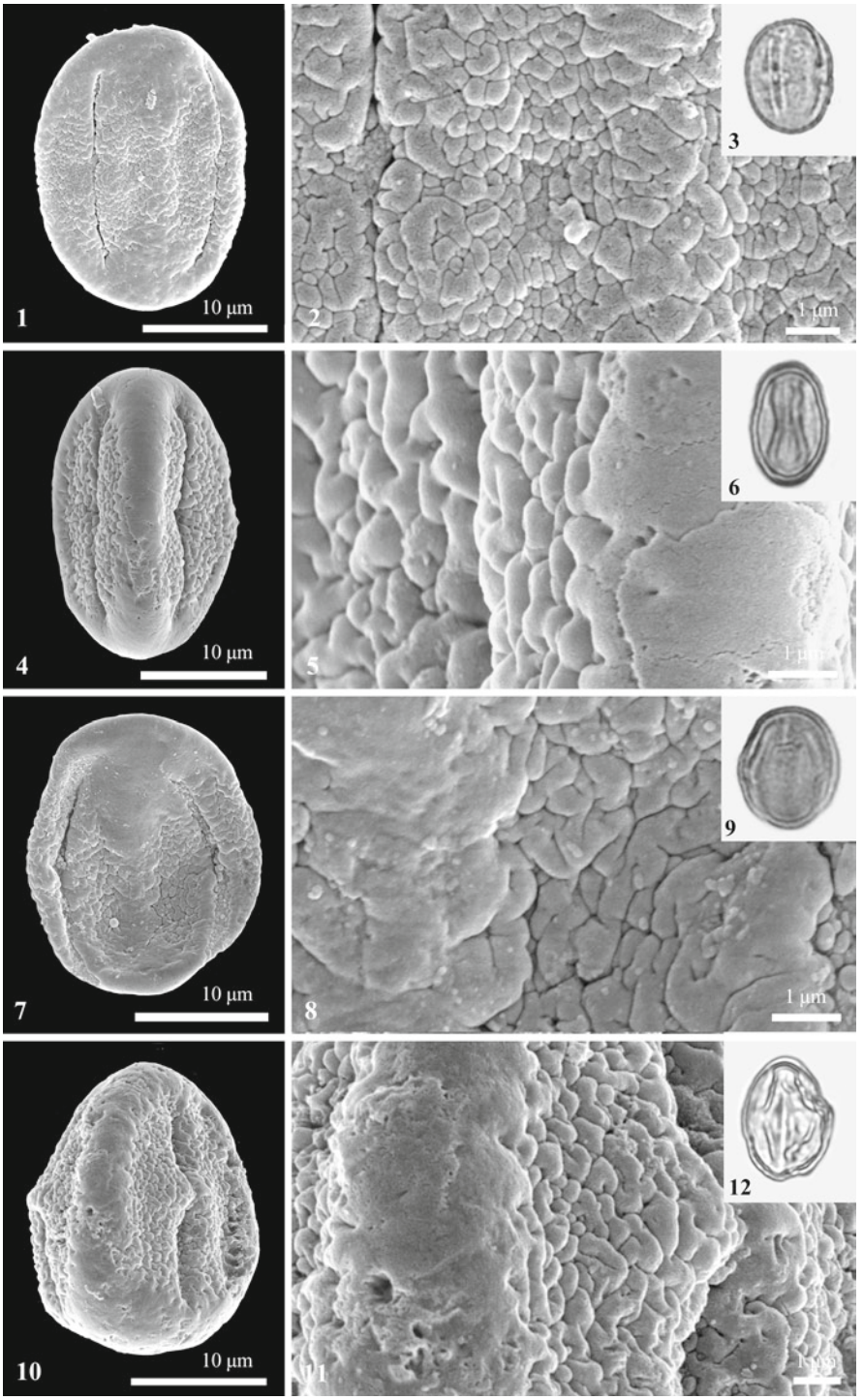



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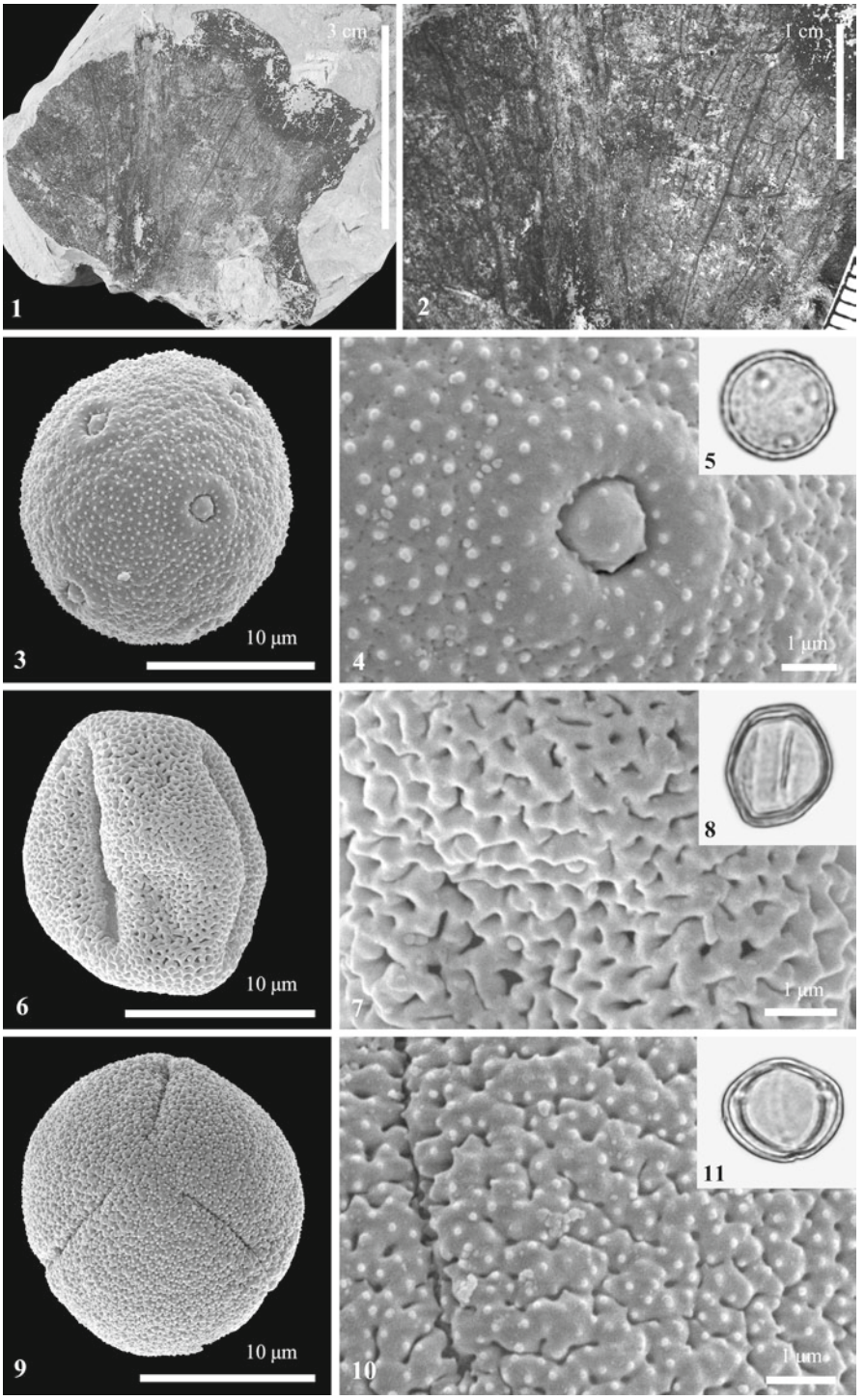



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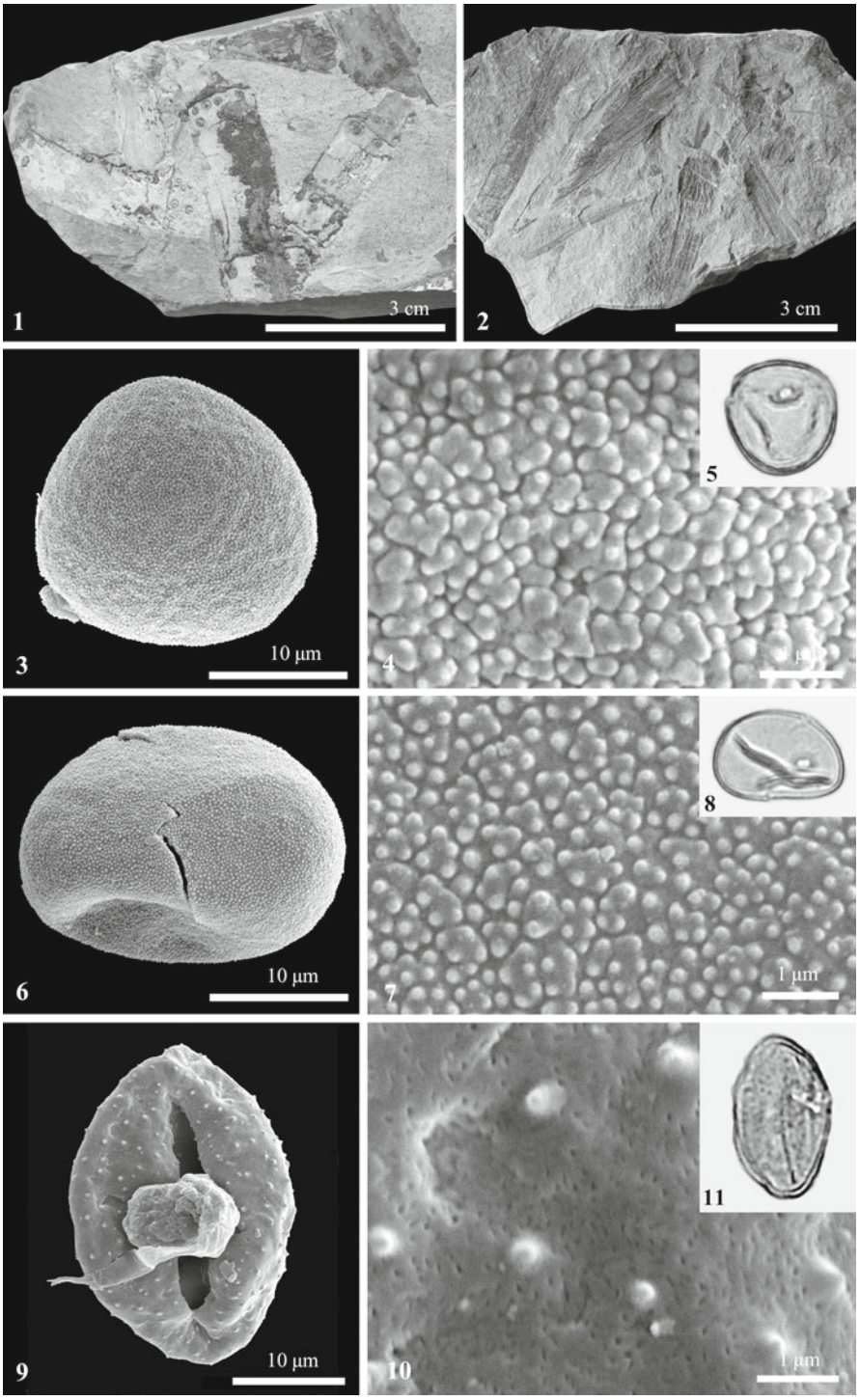



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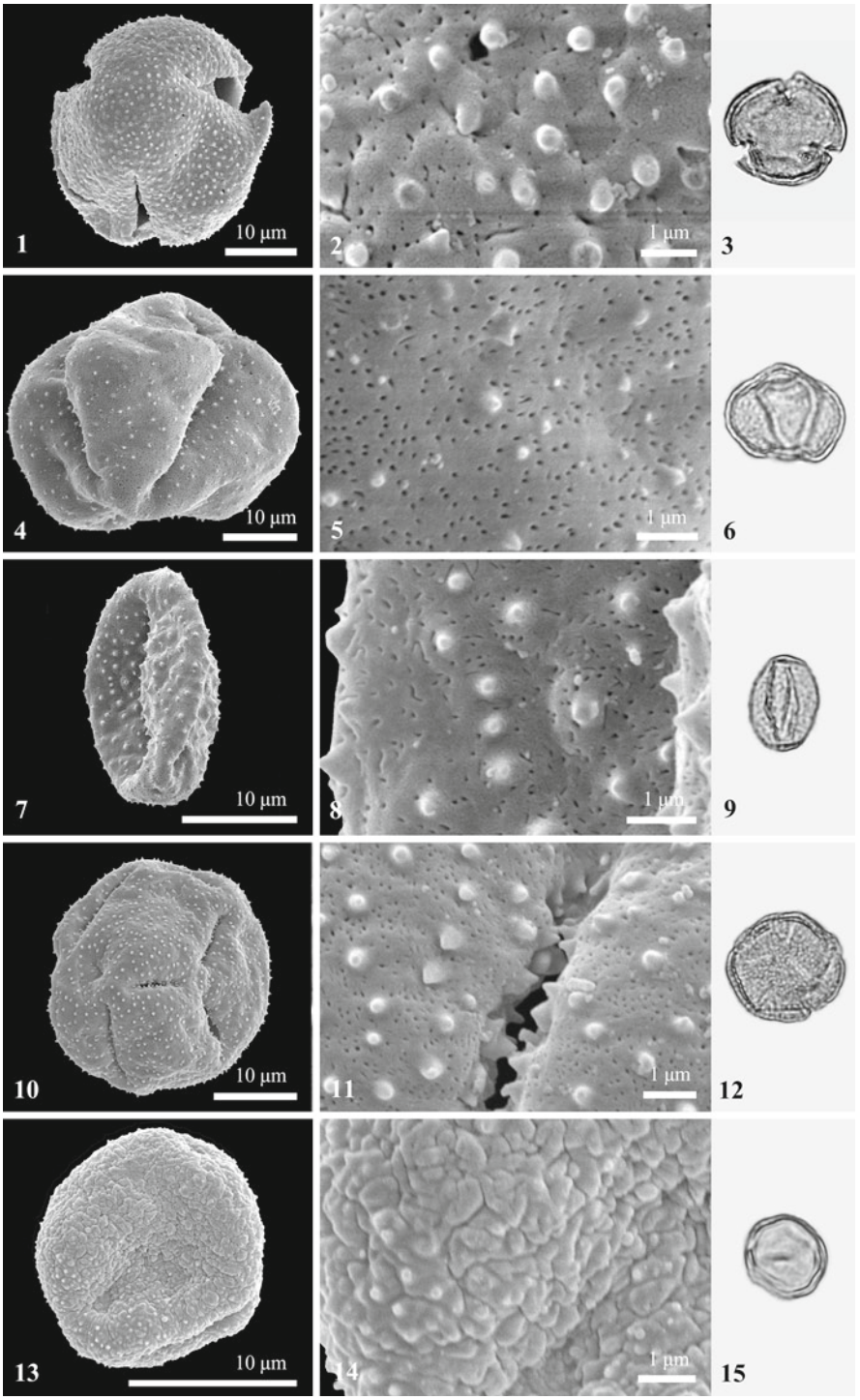

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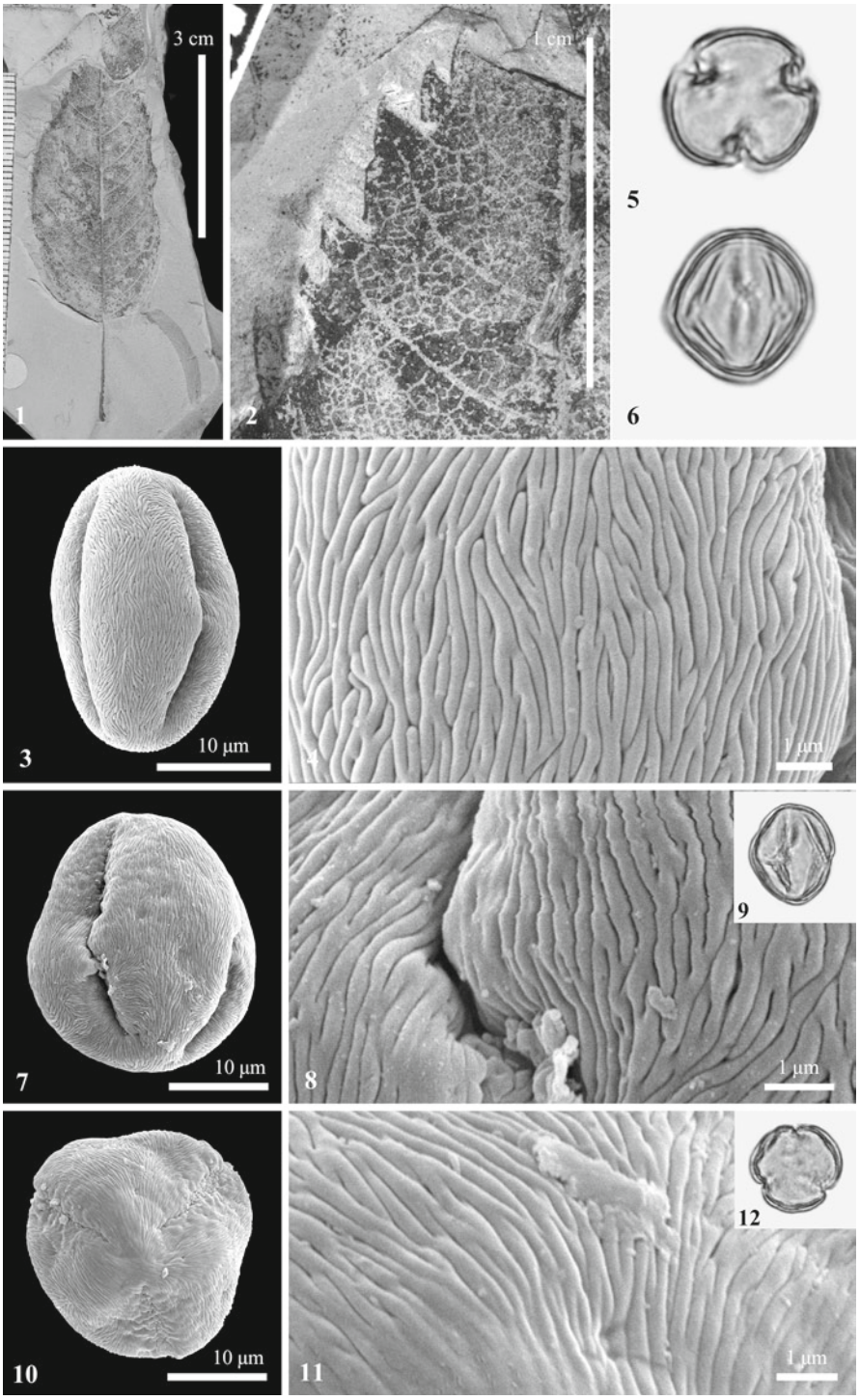



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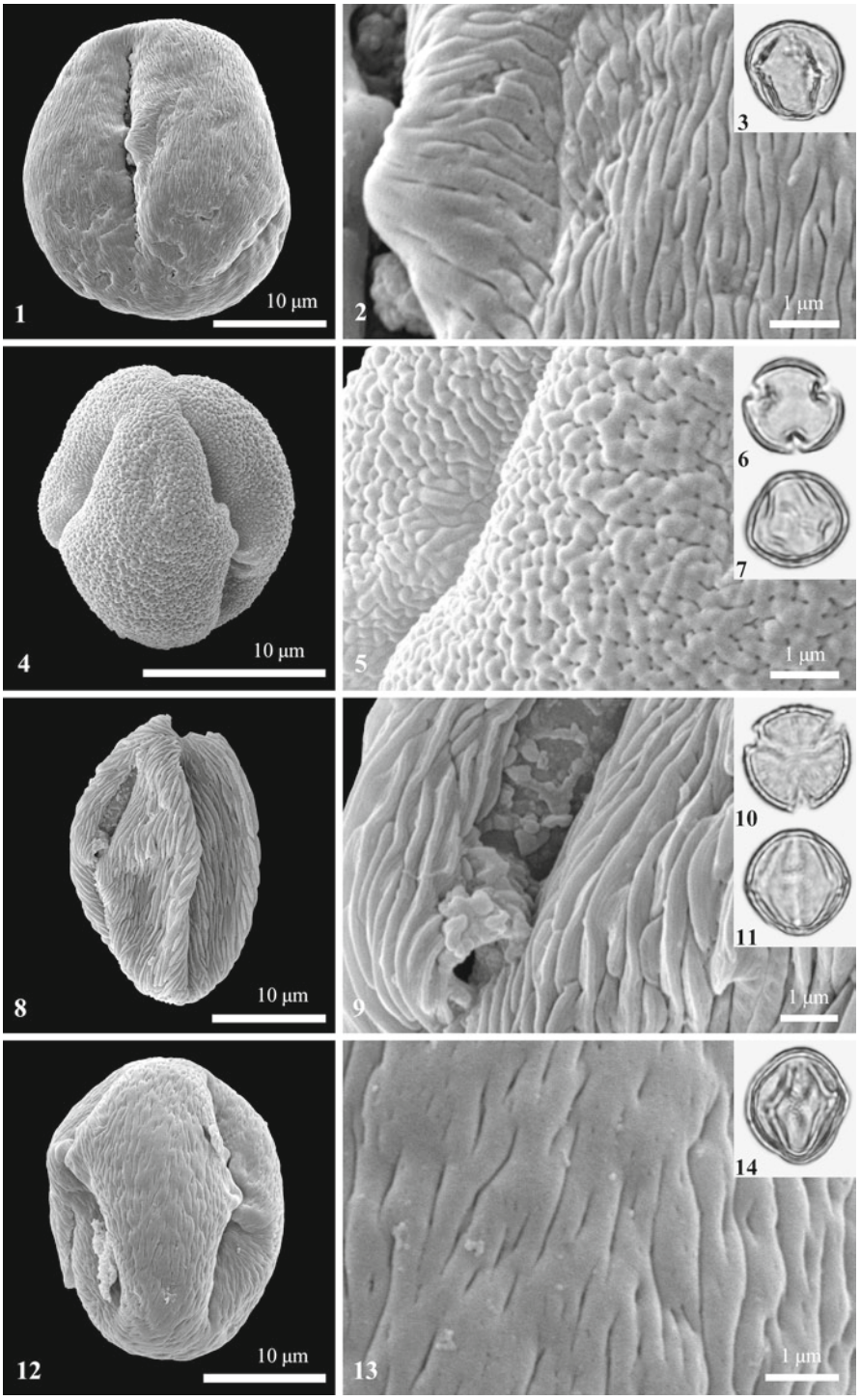



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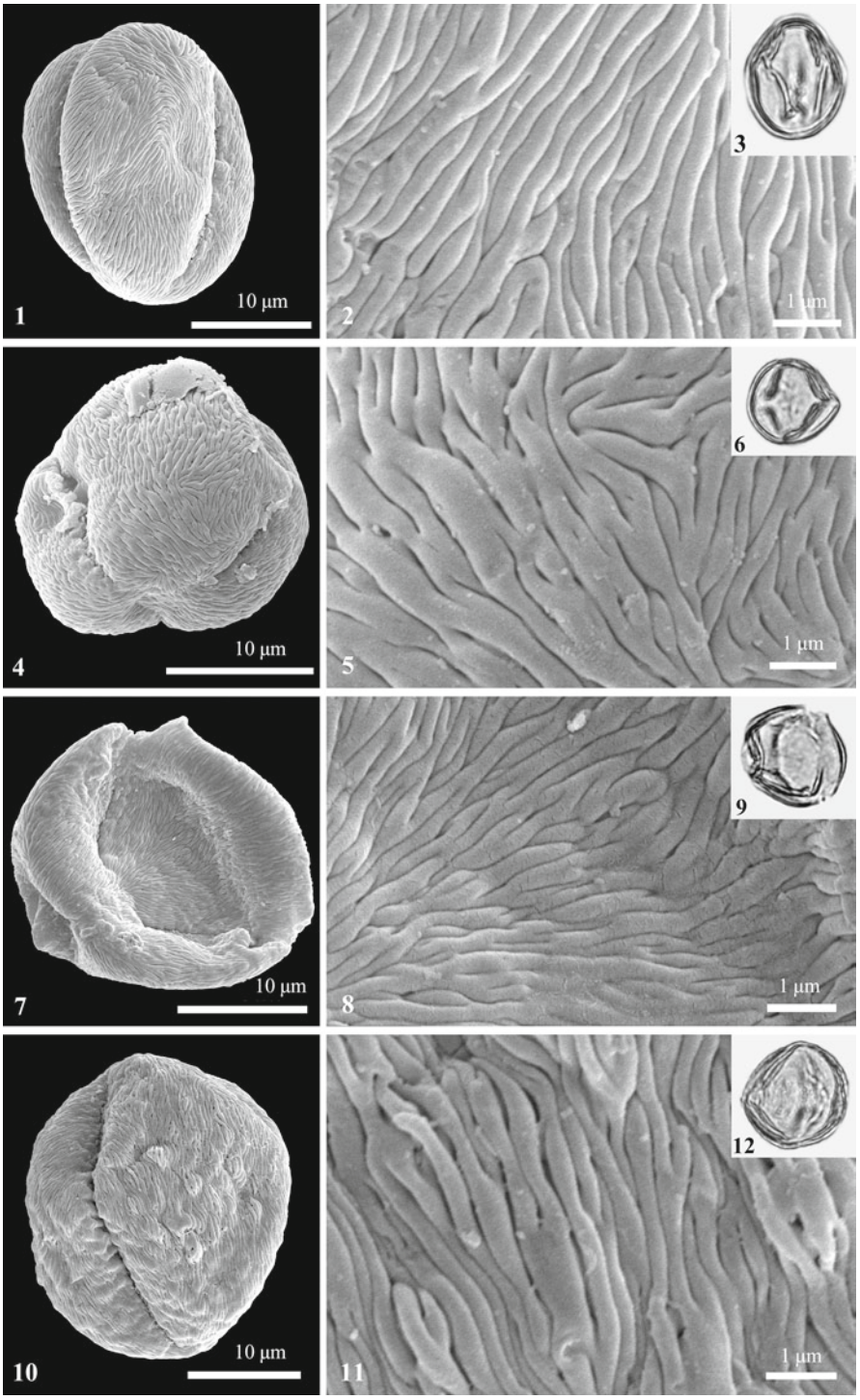



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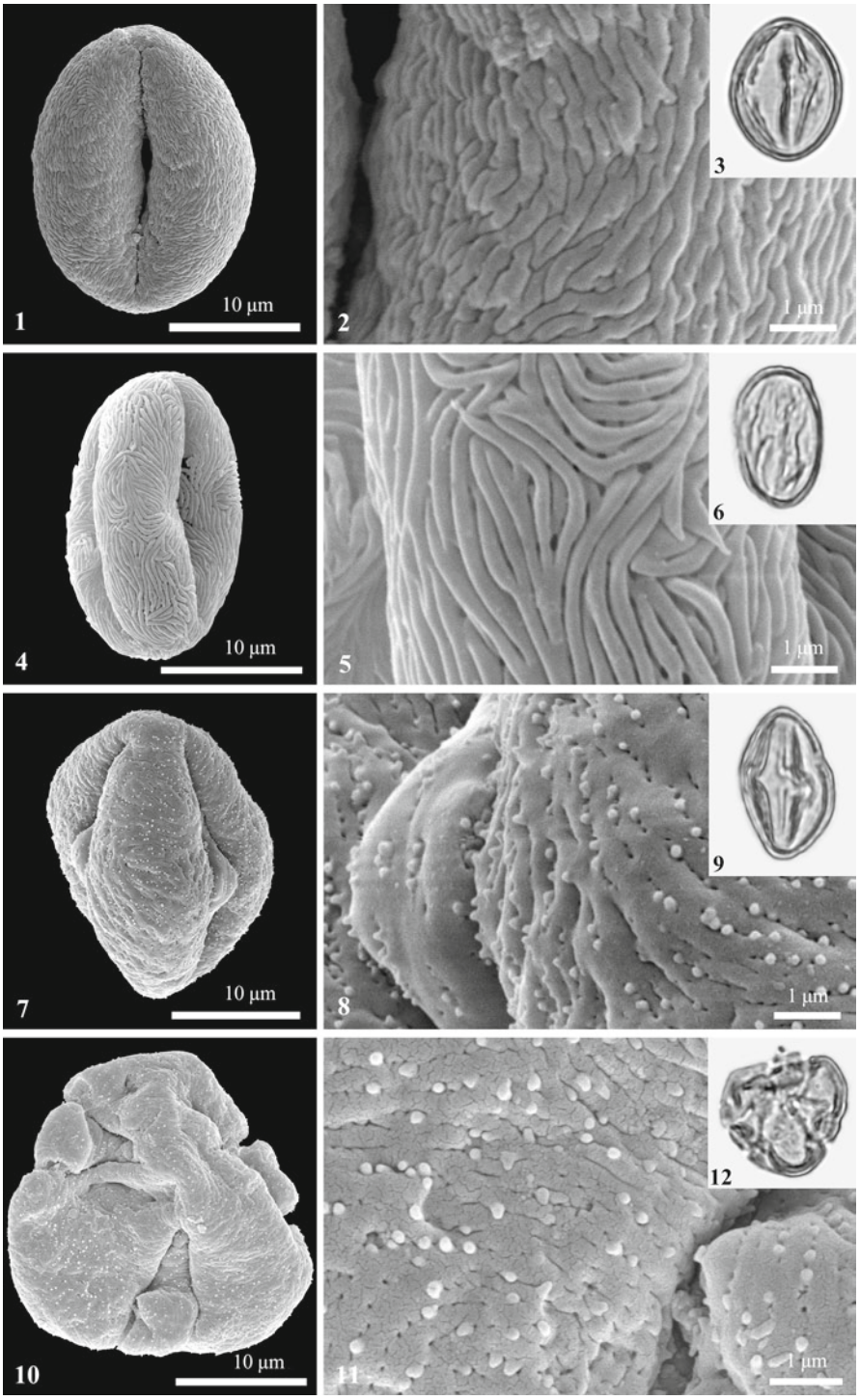



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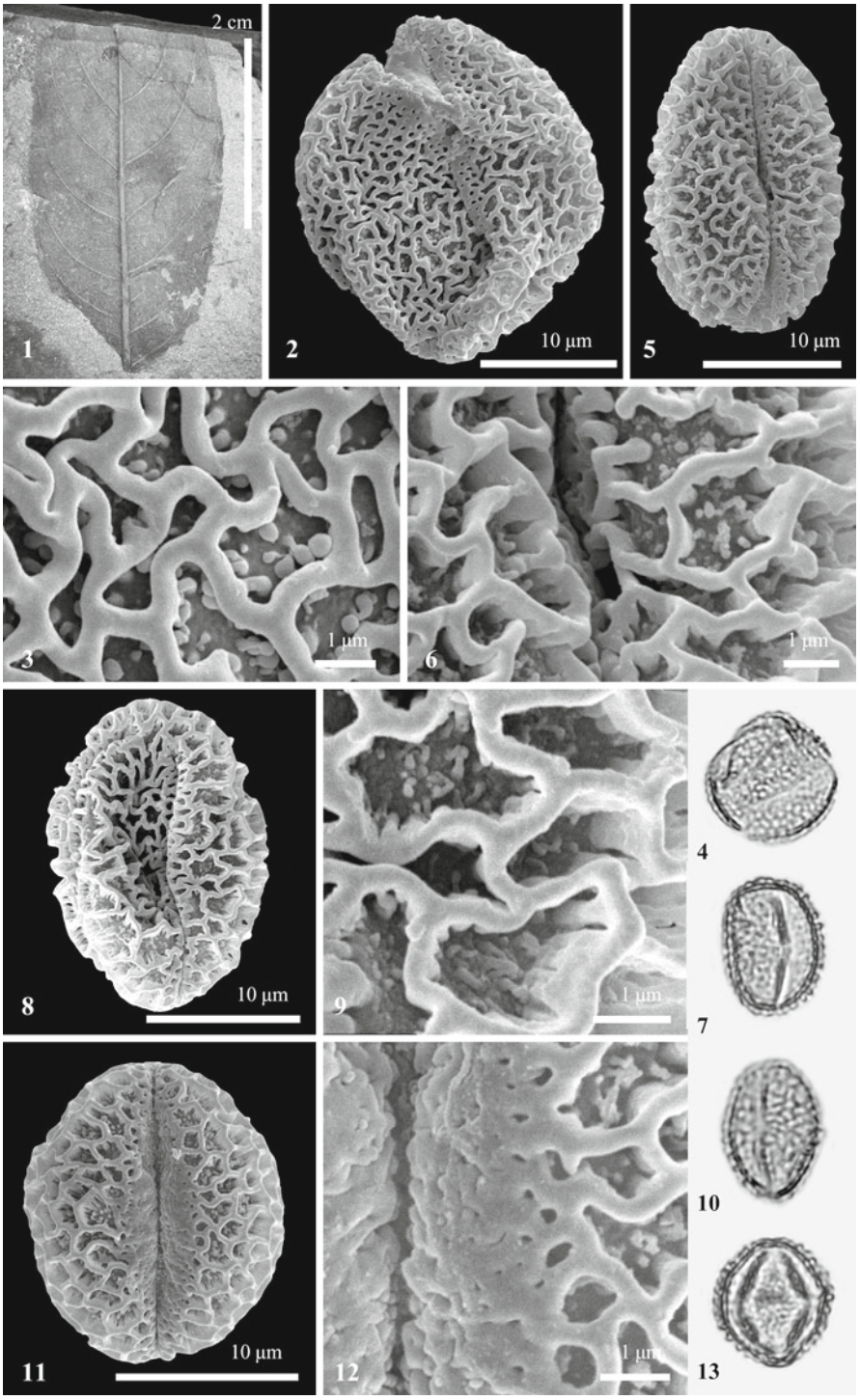



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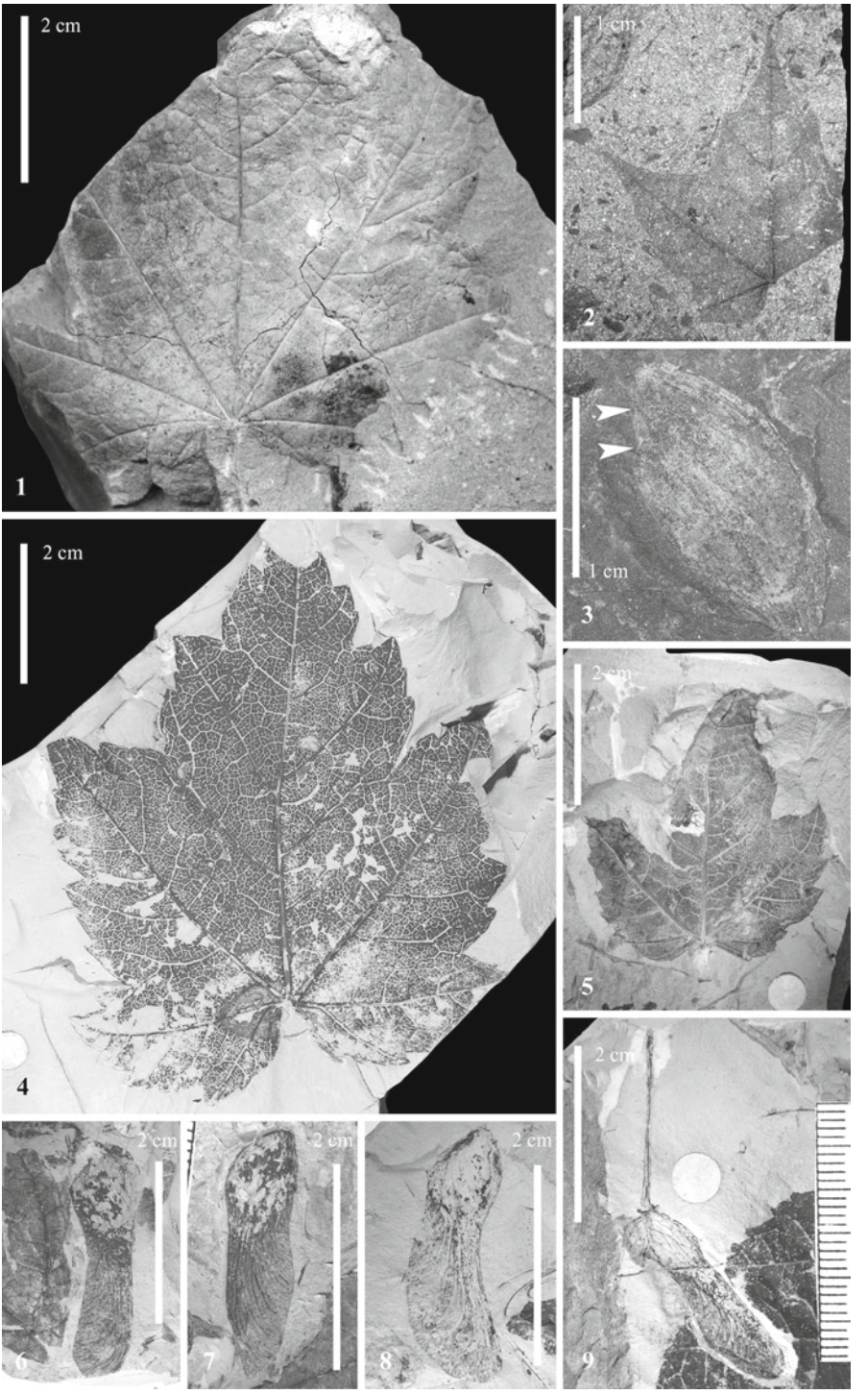



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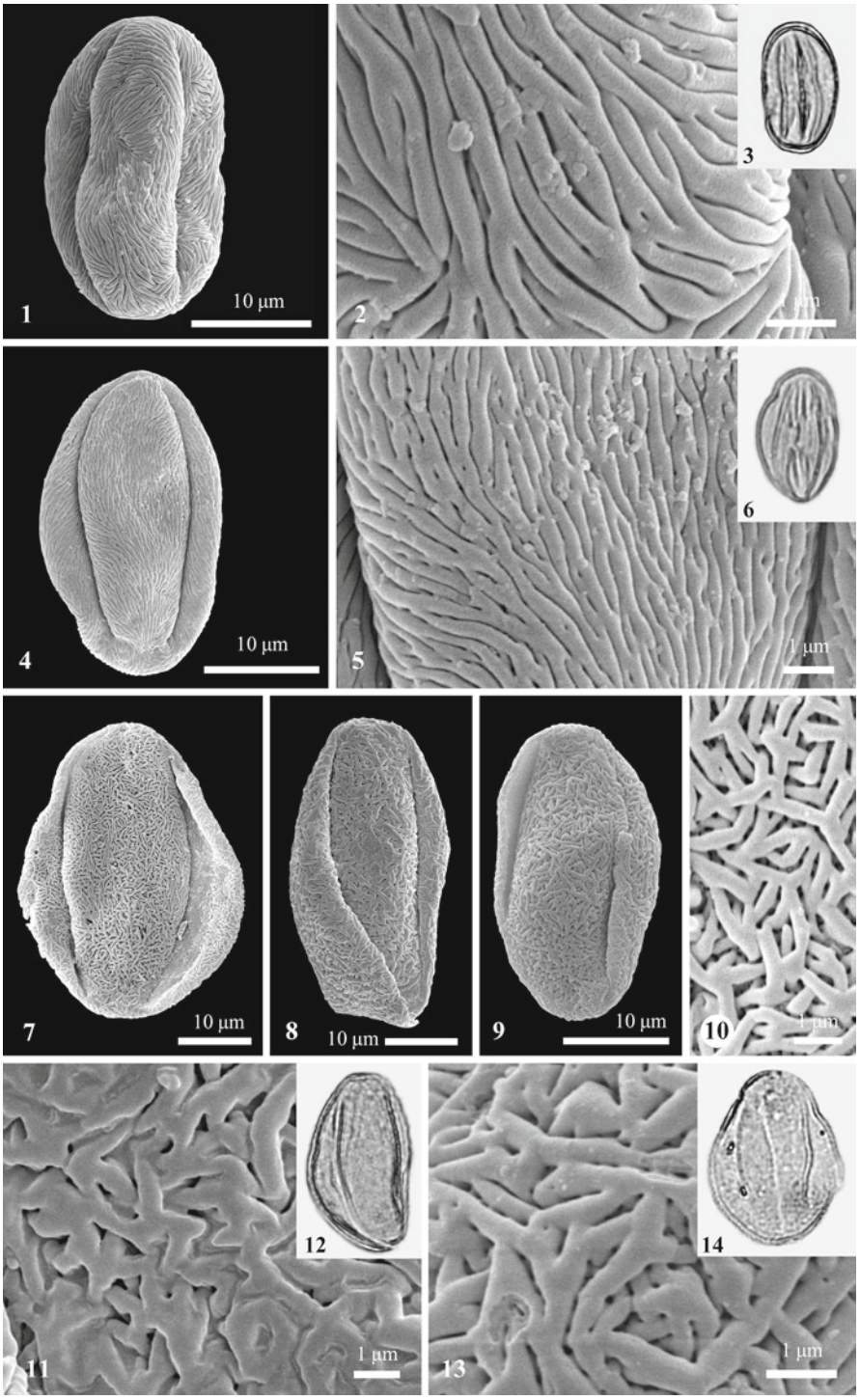

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**Plate 6.41**

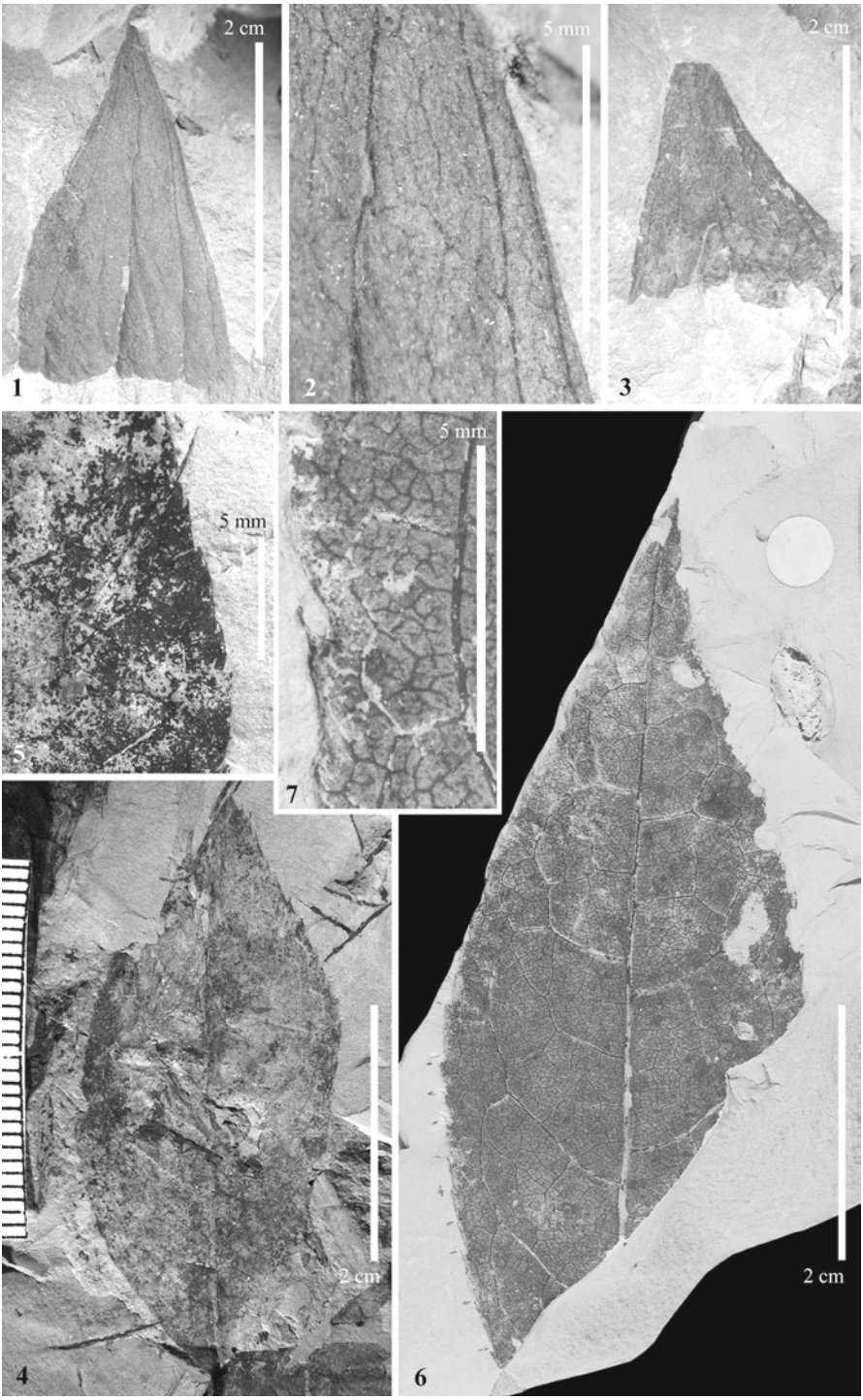



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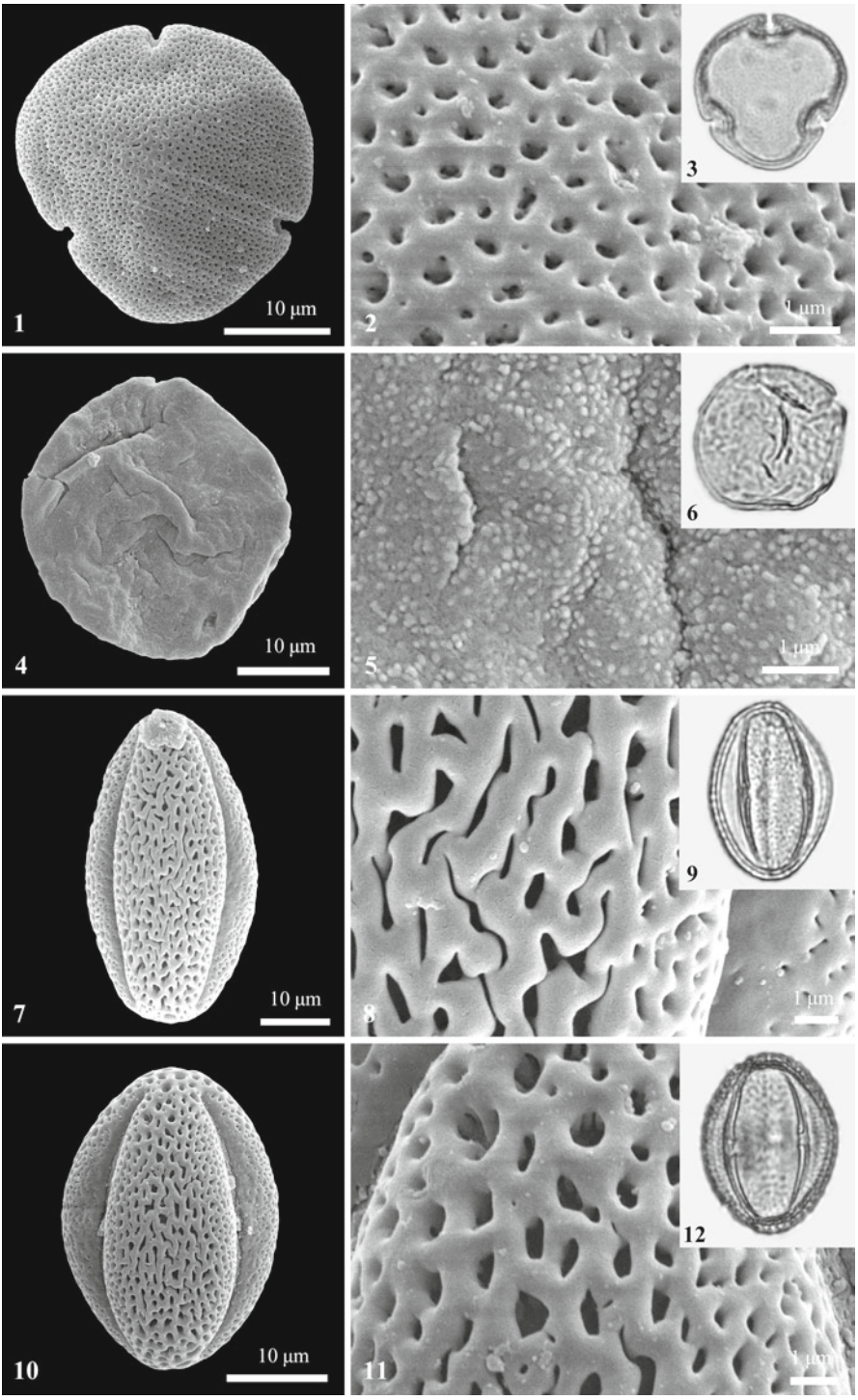



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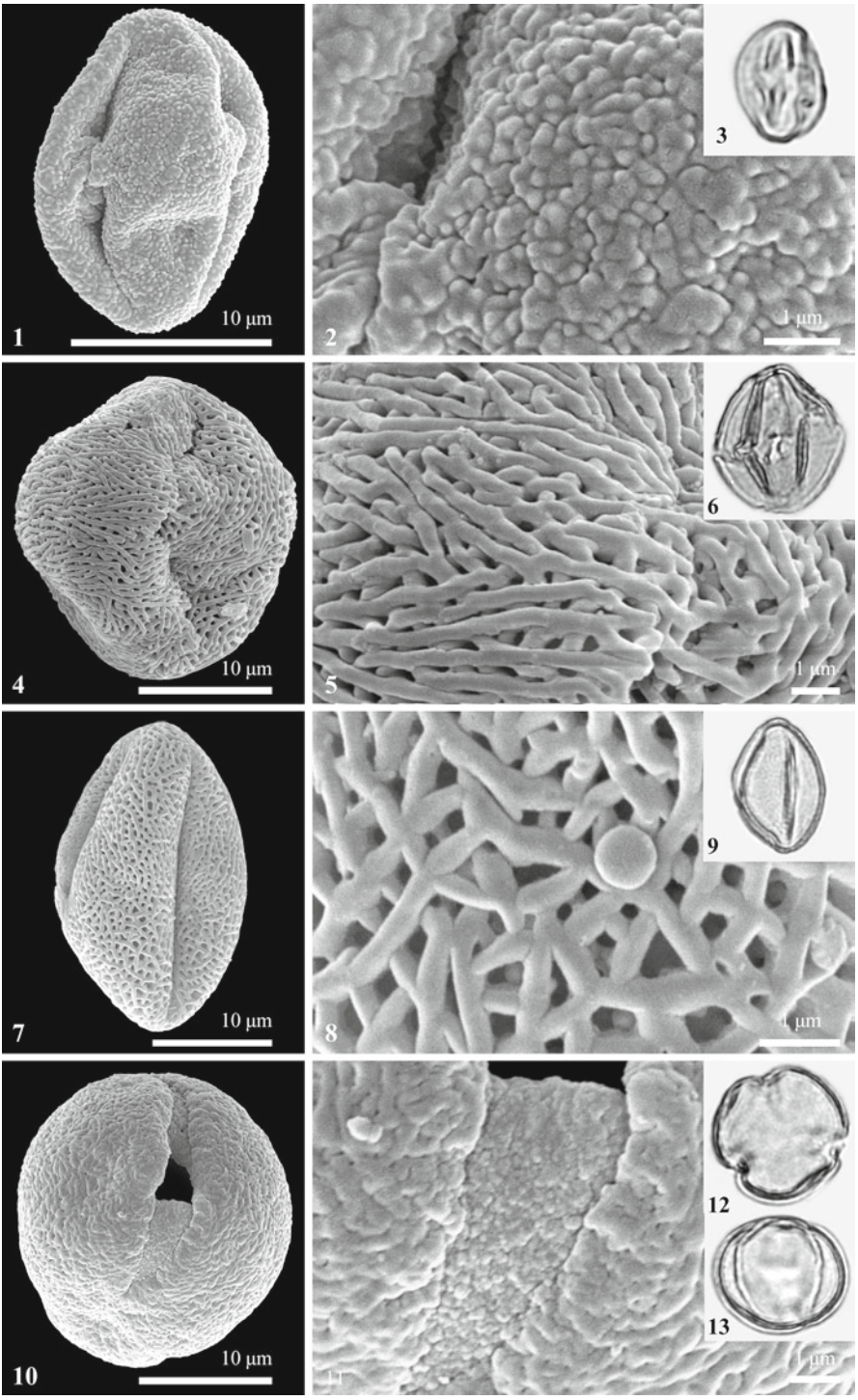



**Plate 6.44**

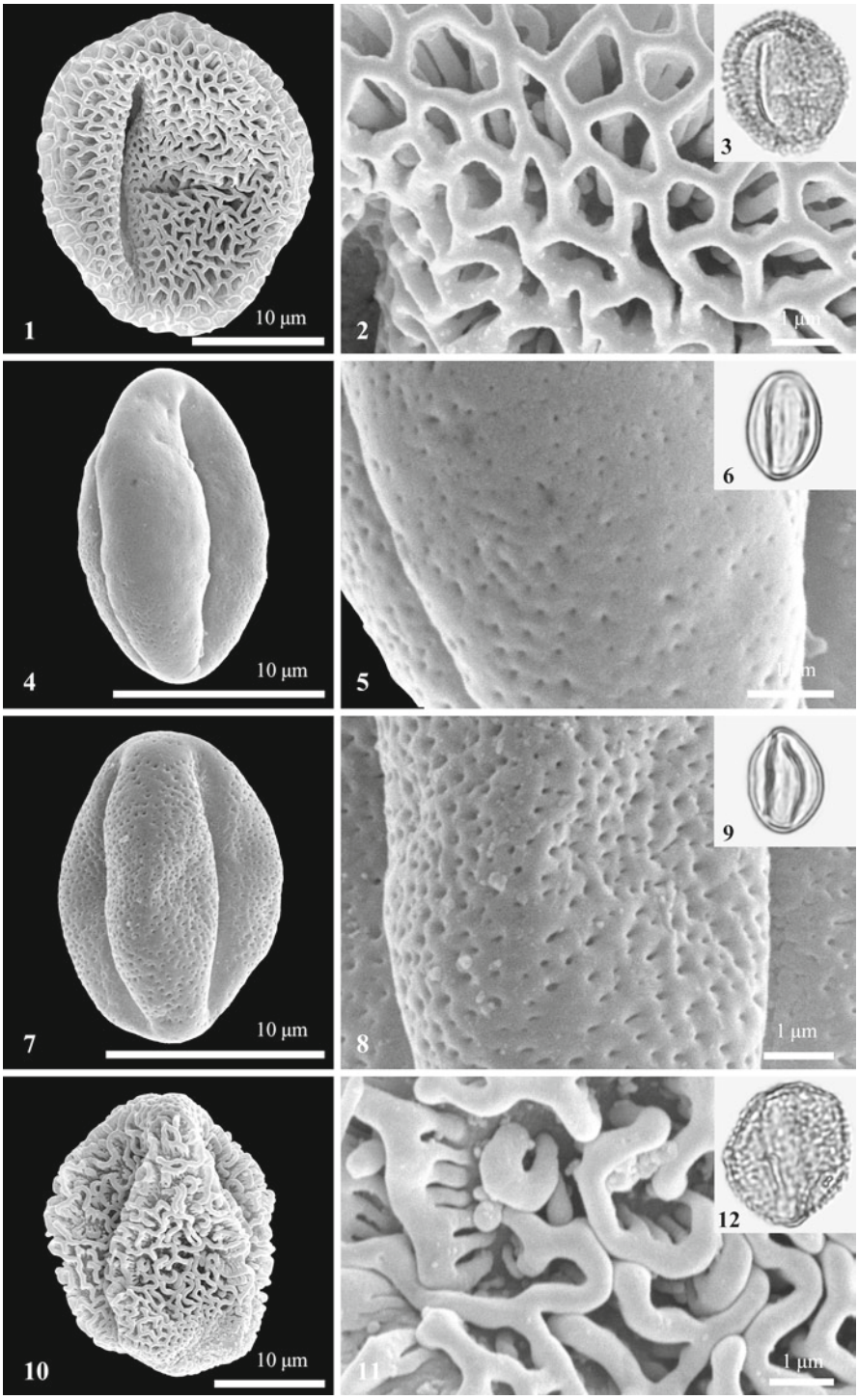



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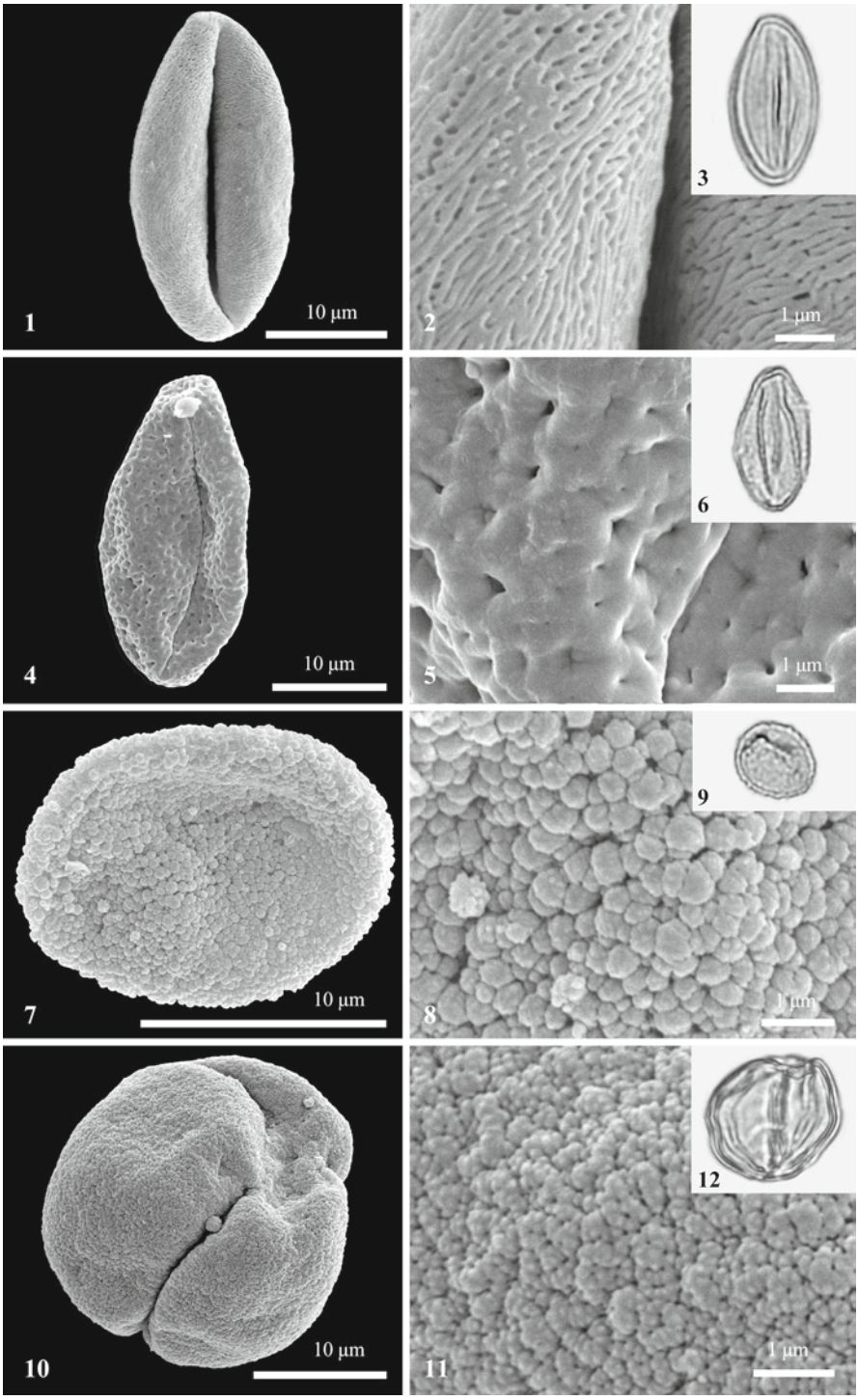



**Plate 6.46**

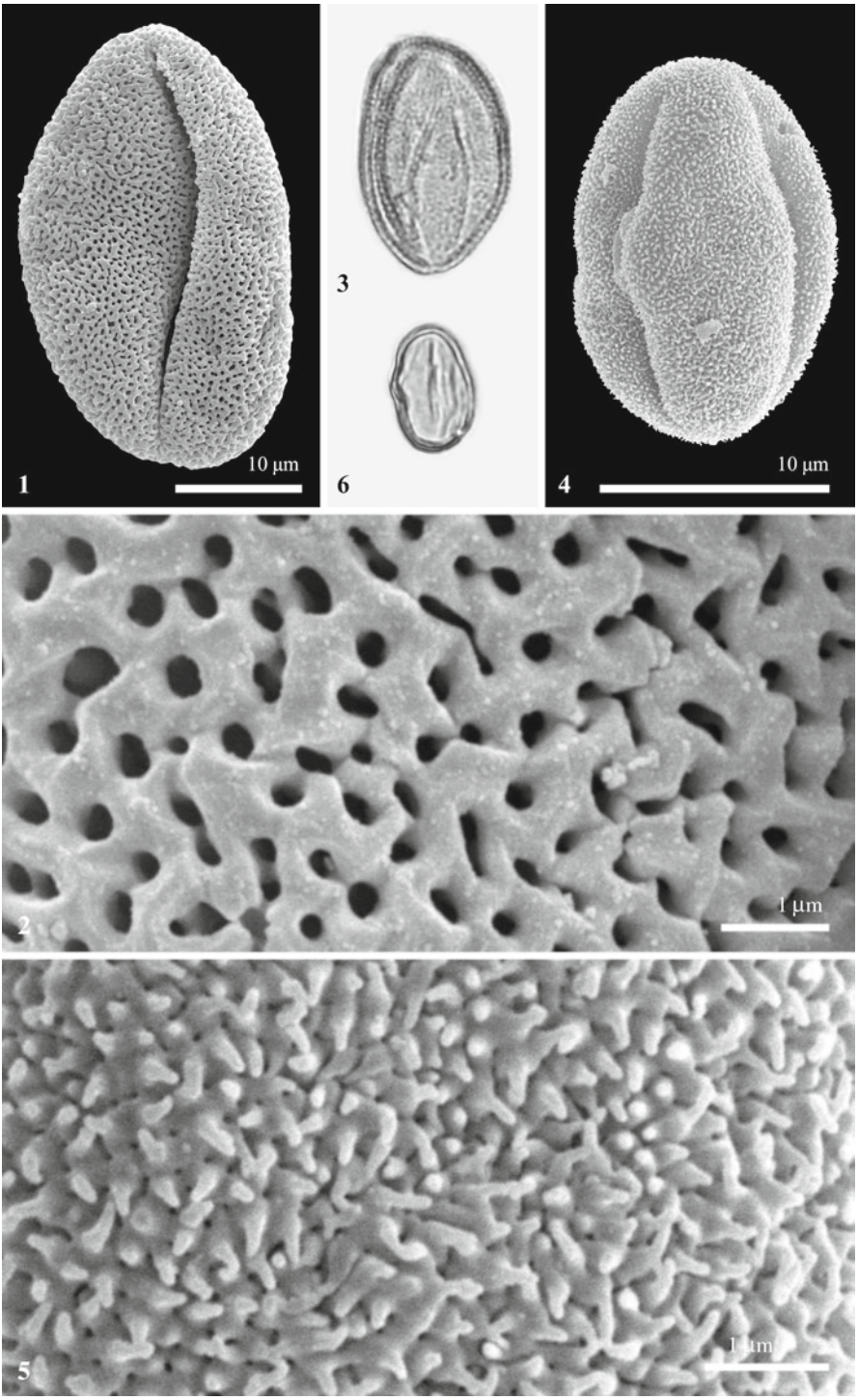



**Plate 6.47**

# Chapter 7
# The Middle Late Miocene Floras – A Window into the Regional Vegetation Surrounding a Large Caldera

**Abstract** Terrestrial fossils from Late Miocene sediments in the Mókollsdalur area are mainly known for their insect fauna. Plant fossils and the sedimentological context suggest that most of the macrofossils deposited at Mókollsdalur originate from trees and shrubs that grew on the slopes around a caldera lake in the highlands. Abundant fossils of aquatic crustaceans, insects, and plants suggest that the lake and adjacent areas were a diverse ecosystem at the time of deposition. Forests covering the slopes were dominated by *Fagus* with a few evergreen elements in the understorey (*Ilex, Rhododendron*). In contrast, the palynological record points to the presence of mixed oak forests in areas behind the mountain ridge surrounding the caldera. The poor representation of herbaceous elements in the pollen record may point to a filter effect against pollen influx from surrounding areas into the lake. Slope exposure may have determined the presence of *Fagus* or *Quercus* as is also seen today in cool temperate regions of the northern hemisphere. Overall, the climate appears to be more diversified than in the older floras with relatively warmer humid conditions windward of the mountains or in sheltered areas close to the lake and cooler more continental conditions leeward of the mountains.

## 7.1 Introduction

The sedimentary rocks of the Skarðsströnd-Mókollsdalur Formation are between 9 and 8 Ma (middle to late Tortonian, middle Late Miocene; McDougall et al. 1984). Sedimentary rocks of this formation were discovered in the late nineteenth century by Thoroddsen (1896) when he studied the lignites of the Northwest Peninsula. The full extension of this formation was later established by Bárðarson (1918), Schwarzbach (1955), and particularly Akhmetiev et al. (1978). Although the presence of well-preserved plant fossils, especially leaves, in this formation was already known from the reports of Bárðarson (1918), Schwarzbach (1955), and Áskelsson (1961), leaf fossils were not described and figured before the 1970s (Friedrich et al. 1972; Akhmetiev et al. 1978; Friedrich and Símonarson 1982; Símonarson and Friedrich 1983; Denk et al. 2005; Grímsson and Denk 2005). The Skarðsströnd-Mókollsdalur Formation has become well-known mainly because of its

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animal fossils, which are generally very rare in Miocene sediments of Iceland. From Mókollsdalur, several nicely preserved insects have been found (Friedrich et al. 1972), but only a single taxon has been described, the hickory aphid, *Longistigma caryae* Harris (Heie and Friedrich 1971). Water fleas, aquatic crustaceans, most likely representing species of *Daphnia*, are also abundant (Símonarson 1981).

In this chapter, we use evidence from plant macrofossils, pollen and spores to reconstruct the vegetation in Iceland 9–8 Ma. The Late Miocene vegetation of Iceland is compared to modern vegetation types, and for some key taxa, ecological and climatic requirements are estimated using their potential modern analogues. Based on this, the climate for Iceland in the middle Late Miocene is evaluated and illustrated with climate diagrams.

Taxonomic affinities of fossil taxa from Iceland to coeval fossils in Eurasia and North America are established and used to describe patterns of plant migration to Iceland during the Late Miocene. The availability of a land bridge between Iceland and Europe/North America during this time period is evaluated in view of the palaeobotanical record.

## 7.2 Geological Setting and Taphonomy

The Skarðsströnd-Mókollsdalur Formation (9–8 Ma; McDougall et al. 1984) is exposed at the southeastern part of the Northwest Peninsula (Fig. 7.1a) and is the youngest fossiliferous sedimentary rock formation exposed there. This formation can be traced along outcrops from southwest to northeast (Fig. 7.1b) along the Skarðsströnd coastline (Tindafjall locality), into Gilsfjörður fjord and up the Brekkudalur valley, over the Steinadalsheiði highland, down into Mókollsdalur (Hrútagil locality, Fig. 7.1c) and Þrúðardalur on the Kollafjörður fjord, and onwards to Ennishöfði (Broddanes locality). The sedimentary rocks composing this formation are quite variable, mostly sandstones and siltstones with associated lignites. The thickness ranges from 5 to 35 m in general (Akhmetiev et al. 1978), except for at the Hrútagil locality and other outcrops in the Mókollsdalur valley, where the sedimentary rocks are over 120 m thick (Friedrich et al. 1972; Grímsson and Símonarson 2006).

Hrútagil in Mókollsdalur is the most important locality of this formation and has the highest number of plant macrofossils. Otherwise, identifiable plant remains are rarely found outside the Mókollsdalur area, and the same is true for animal fossils. The lowest part of the sedimentary rocks in Hrútagil is composed of thick hyaloclastite units with interlaminated breccias and sandstones. The middle part is mostly composed of sandstones and siltstones, and in the upper part siltstones, claystones and organic-rich sediments become prominent, both diatomite and lignites. It is in this upper part where most of the plant and animal fossils have been collected. The whole section is interlaminated by various types of volcanic sediments, reflecting a rather frequent eruption history during accumulation.

Tectonic displacement, volcanic constructions, and sedimentary rock types in the Mókollsdalur valley and the Hrútagil gully reflect the palaeo-topography and the most important geological features in the area during time of accumulation.

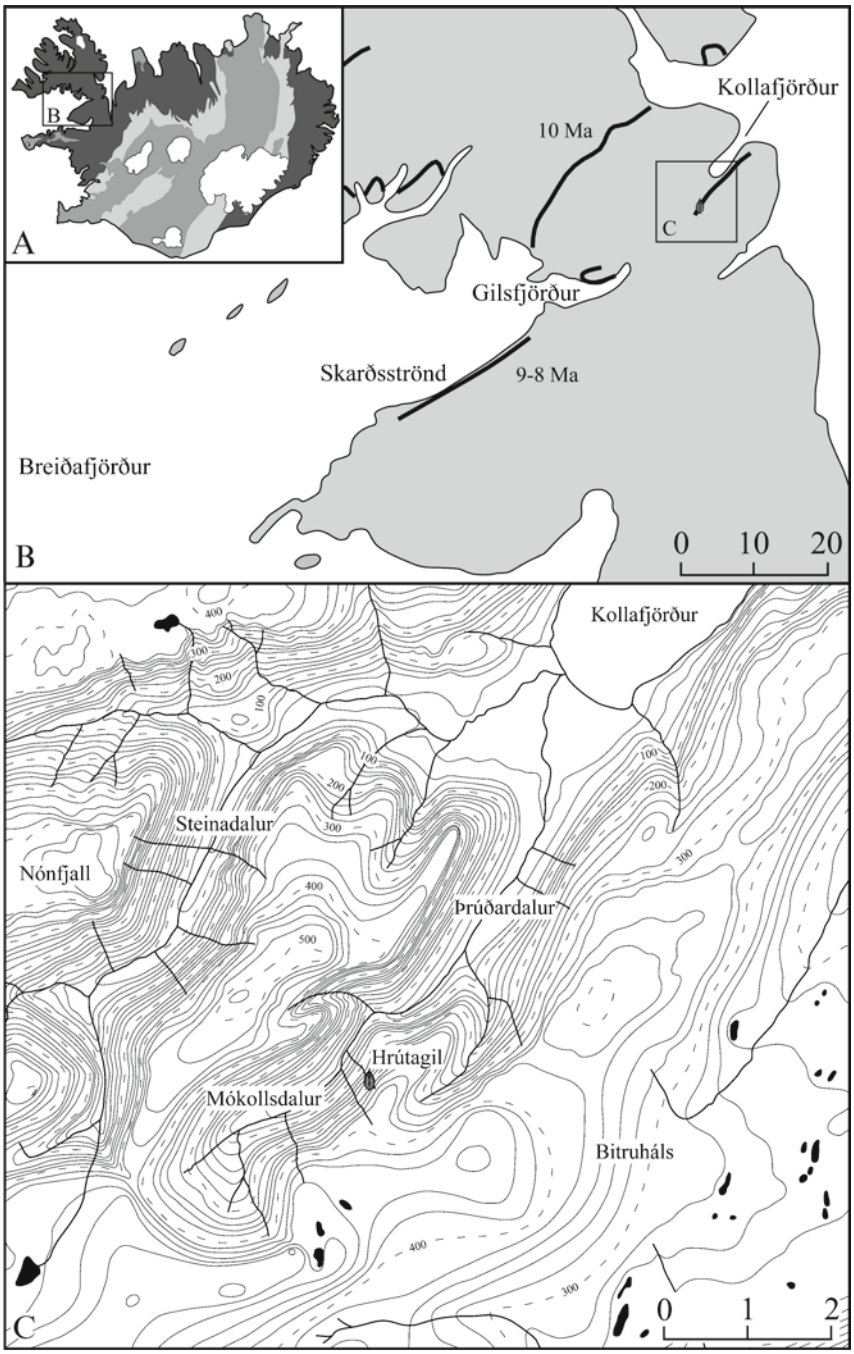



**Fig. 7.1** Map showing fossiliferous localities of the 9–8 Ma formation. (**a**) bedrock geology (see Fig. 1.10 for explanation), (**b**) extension of sedimentary rock formation, (**c**) Hrútagil locality (Geological background modified after Jóhannesson and Sæmundsson 1989; altitudinal lines from Landmælingar Íslands 1994)

Various indications point to the presence of an extinct volcanic system with a central volcano in the area surrounding the Mókollsdalur, Þrúðardalur, and Steinadalur valleys (Fig. 7.1c). First, intermediate intrusions with associated radiating dykes and fault swarms are seen around Mókollsdalur (Jóhannesson and Sæmundsson 1989). Second, acid and intermediate volcanic sedimentary units are preserved as various tuff types in the area (Friedrich et al. 1972; Akhmetiev et al. 1978). This central volcano was a large caldera (Jóhannesson and Sæmundsson 1998) and the sediments seen in Hrútagil and other outcrops in Mókollsdalur accumulated in the freshwater lake of this caldera. Judging from the geography and geological history of the area, the caldera was positioned in the highlands at a considerable distance from the coast when it was active. The freshwater lake in the central part of the caldera was bound by a steep cliff and surrounded by a mountain ridge formed by the eruptions. Macrofossil plant remains in the sediments of this caldera originate from trees and shrubs growing on the hillsides and slopes facing the lake of the caldera. In contrast, the palynological record captures not only the vegetation surrounding the caldera lake, but also outside the caldera. Apparently, the lake was a diversified ecosystem as reflected by the repeated diatomite units and the frequently found water fleas in the upper part of the sedimentary rock sequence in Hrútagil and Mókollsdalur.

## 7.3 Floras, Vegetation, and Palaeoenvironments

The floras of the Skarðsströnd-Mókollsdalur Formation are markedly less species-rich than those from the older Tröllatunga-Gautshamar Formation (42 versus 99 taxa; Table 7.1, Fig. 7.2, Plates 7.1–7.23). Most fossil taxa belong to woody angiosperms (19 taxa), followed by mosses and ferns (eight taxa) and conifers (nine taxa). The low number of herbaceous plants (five taxa) is probably the result of taphonomic processes rather than a reflection of the lack of herbaceous vegetation.

**Table 7.1** Taxa recorded for the 9–8 Ma floras of Iceland

| Skarðsströnd-Mókollsdalur Formation<br>Taxa | Pollen | Leaves | RP | DM |
|---|---|---|---|---|
| Lycopodiaceae | | | | |
| *Lycopodiella* sp. | + | | | 1a |
| *Lycopodium* sp. | + | | | 1a |
| *Huperzia* sp. | + | | | 1a |
| Osmundaceae | | | | |
| *Osmunda* sp. | + | | | 1a |
| Polypodiaceae | | | | |
| Polypodiaceae gen. et spec. indet. 1 | + | | | 1a |
| Polypodiaceae gen. et spec. indet. 6 | + | | | 1a |
| Incertae sedis – unassigned spores | | | | |
| Monolete spore, fam., gen. et spec. indet. 1 | + | | | 1a |
| Monolete spore, fam., gen. et spec. indet. 2 | + | | | 1a |

(continued)

**Table 7.1** (continued)

| Skarðsströnd-Mókollsdalur Formation<br>Taxa | Pollen | Leaves | RP | DM |
|---|---|---|---|---|
| Pinaceae | | | | |
| *Abies* sp. | + | | | 2a |
| *Larix* sp. | + | | | 2a |
| *Picea* sect. *Picea* | + | | + D | 2a |
| *Pinus* sp. 1 (Diploxylon type) | + | | | 2a |
| *Pinus* sp. 2 (Haploxylon type) | + | | | 2a |
| *Pseudotsuga* sp. | + | | + | 2a |
| *Tsuga* sp. 1 | + | | | 2a |
| *Tsuga* sp. 2 | + | | | 2a |
| Sciadopityaceae | | | | |
| *Sciadopitys* sp. | + | | | 2a |
| Apiaceae | | | | |
| Apiaceae gen. et spec. indet. 5 | + | | | 1b |
| Aquifoliaceae | | | | |
| *Ilex* sp. 2 | + | | | 1b |
| Asteraceae | | | | |
| Asteraceae gen. et spec. indet. 1 | + | | | 1a |
| Betulaceae | | | | |
| *Alnus cecropiifolia* | + | **+** | + D | 1a, 2a |
| *Betula cristata* | + | **+** | + D | 1a |
| cf. *Carpinus* | | + | | 2a |
| Calycanthaceae | | | | |
| aff. Calycanthaceae | + | | | 1b |
| Cornaceae | | | | |
| *Cornus* sp. | | + | | 1b |
| Ericaceae | | | | |
| *Rhododendron* sp. 2 | + | | | 1a?, 2a |
| Fagaceae | | | | |
| *Fagus gussonii* | + | **+** | + D | 2b, 3 |
| *Quercus* infrageneric group *Quercus* sp. 1 | + | | | 2b, 3 |
| Juglandaceae | | | | |
| *Cyclocarya* sp. | (+) | + | | 2a |
| *Pterocarya* sp. | (+) | + | + D | 2a |
| Myricaceae | | | | |
| *Myrica* sp. | + | | | 1b |
| Poaceae | | | | |
| Poaceae gen. et spec. indet. 1 | + | | | 1b, 2a |
| Ranunculaceae | | | | |
| *Thalictrum* sp. 2 | + | | | 1b |
| Ranunculaceae gen. et spec. indet. 2 | + | | | 1b |
| Salicaceae | | | | |
| *Salix gruberi* | | **+** | | 1a |
| Sapindaceae | | | | |
| *Acer crenatifolium* subsp. *islandicum* | (+)2 | **+** | **+ D** | 2a |
| *Acer askelssonii* | (+)2 | + | + D | 2a |
| Trochodendraceae | | | | |
| *Tetracentron atlanticum* | **+** | **+** | | 2a |

(continued)

**Table 7.1** (continued)

| Skarðsströnd-Mókollsdalur Formation<br>Taxa | Pollen | Leaves | RP | DM |
|---|---|---|---|---|
| Ulmaceae | | | | |
| *Ulmus* section *Ulmus* sp. | + | + | + D | 2a |
| Incertae sedis – Magnoliophyta | | | | |
| *Dicotylophyllum* sp. D | | + | | ? |
| *Dicotylophyllum* sp. E | | + | | ? |
| Angiosperm fam. et gen. indet. A | | | + | ? |

*L* leafy axis, *A* fruit attached to leafy axis, *D* fruit dispersed, *RP* reproductive structure, + organ present, **+** original description of species based on this organ, (+) organ belonging to genus but uncertain to which of the species, (+) 2 indicating number of pollen types possibly belonging to the eponymous morphotaxon, *DM* dispersal mode: *1a* wind long distance (anemochory), *1b* bird long distance (endozoochory), *2a* wind short distance (anemochory), *2b* animals short distance (exozoochory), *3* dyschory

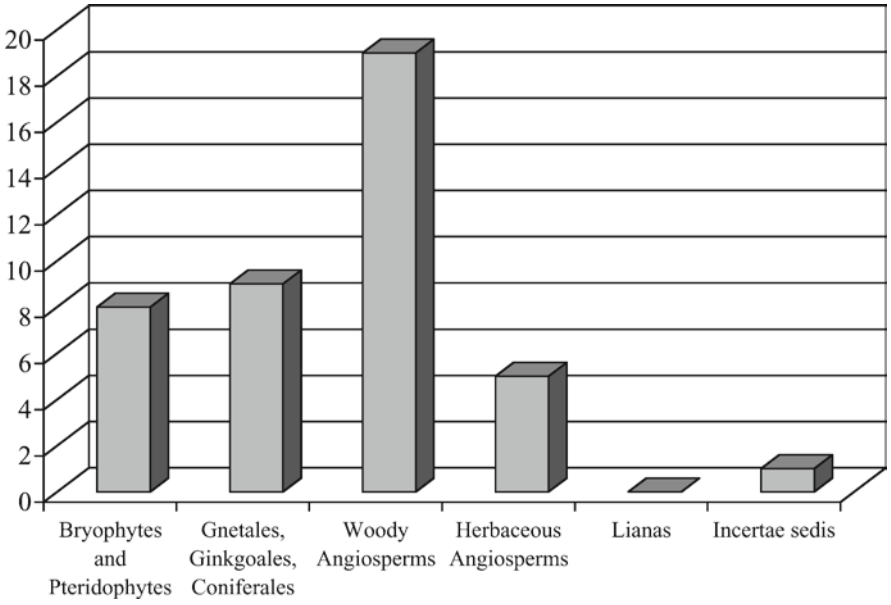



**Fig. 7.2** Distribution of life forms and higher taxa among the plants from the 9–8 Ma formation. Height of columns indicates number of taxa

The mountain ridge surrounding the caldera lake may have provided a vital barrier to pollen influx from outside the caldera. Apart from this bias, the macrofossil and palynological record allows for drawing a fairly precise picture of the palaeovegetation surrounding the caldera in the Mókollsdalur area.

Six vegetation types can be distinguished (Table 7.2; Fig. 7.3). Only a few taxa are typical of flooded areas, possibly suggesting that the lake shores were not inhabited by extensive swamp forests. A poor riparian community may have contained a small number of canopy tree species (*Alnus, Pterocarya*) with some herbaceous ferns, fern allies, and angiosperms in the understorey. Shrubs such as aff.

**Table 7.2** Vegetation types and their components during the middle Late Miocene of Iceland

Vegetation types 9–8 Ma

**Temporally flooded lake margin**

*Lycopodiella* sp.
*Alnus cecropiifolia*
aff. Calycanthaceae
*Myrica* sp.
*Osmunda* sp.
Poaceae gen. et spec. indet. 1
*Pterocarya* sp.
Ranunculaceae gen. et spec. indet. 2
*Salix gruberi*

**Well-drained lowland forests and lake margins**

*Lycopodium* sp.
*Osmunda* sp.
Polypodiaceae gen. et spec. indet. 1, 6
*Picea* sect. *Picea*
*Acer askelssonii*
*Acer crenatifolium* subsp. *islandicum*
*Alnus cecropiifolia*
*Betula cristata*
aff. Calycanthaceae
cf. *Carpinus* sp.
*Cornus* sp.
*Myrica* sp.
*Pterocarya* sp.
*Fagus gussonii*
*Quercus* sp. 1
*Rhododendron* sp. 2
*Ulmus* sp.

**Foothill forests**

*Lycopodium* sp.
Polypodiaceae gen. et spec. indet. 1, 5
*Picea* sect. *Picea*
*Sciadopitys* sp.
*Ilex* sp. 2
*Alnus cecropiifolia*
*Betula cristata*
cf. *Carpinus* sp.
*Rhododendron* sp. 2
*Fagus gussonii*
*Quercus* sp. 1
*Cyclocarya* sp.
*Acer askelssonii*
*Acer crenatifolium* subsp. *islandicum*
*Tetracentron atlanticum*
*Ulmus* sp.

**Montane forests**

*Lycopodium* sp.
Polypodiaceae gen. et spec. indet. 1, 6
*Abies* sp.
*Larix* sp.
*Picea* sect. *Picea*
*Pseudotsuga* sp.
*Tsuga* sp. 1, 2
*Sciadopitys* sp.
*Acer crenatifolium* subsp. *islandicum*
*Cyclocarya* sp.
*Fagus gussonii*
*Ilex* sp. 2
*Rhododendron* sp. 2
*Tetracentron atlanticum*
*Ulmus* sp.

**Meadows and shrublands**

*Huperzia* sp.
Apiaceae gen. et spec. indet. 5
Asteraceae gen. et spec. indet. 1
Poaceae gen. et spec. indet. 1
Ranunculaceae gen. et spec. indet. 2
*Thalictrum* sp. 2

**Rocky outcrop forests**

*Huperzia* sp.
*Lycopodium* sp.
*Larix* sp.
*Picea* sect. *Picea*
*Pinus* sp. 1, 2
*Pseudotsuga* sp.
*Tsuga* sp. 1, 2
*Tetracentron atlanticum*

**AZONAL VEGETATION** | **ZONAL VEGETATION**

The palaeoecology of fossil species is reconstructed from their sedimentological context and ecology of modern analogues

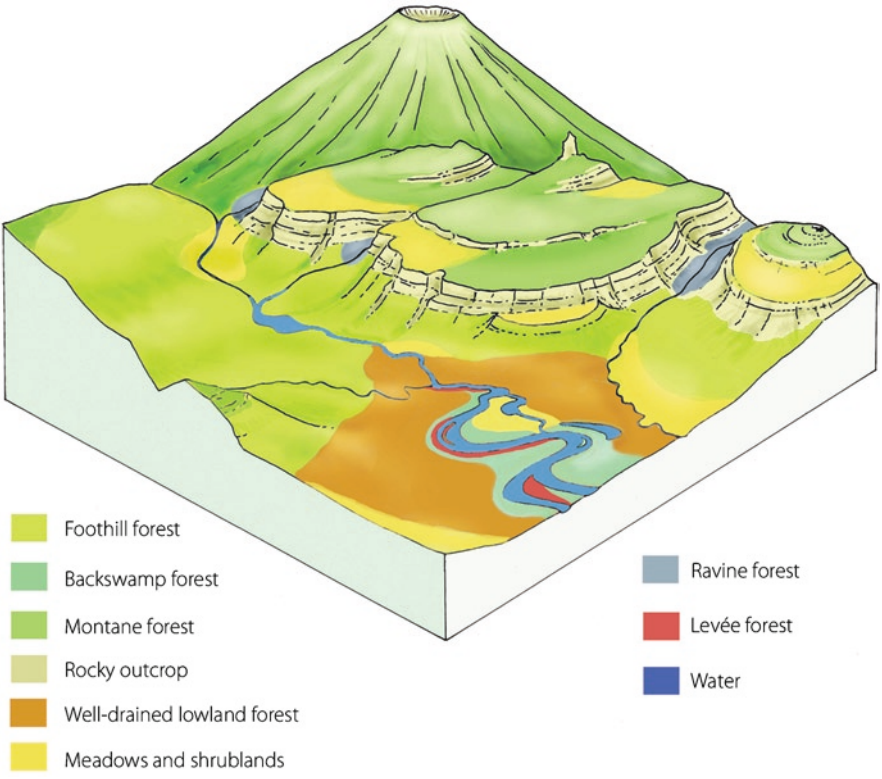



**Fig. 7.3** Schematic block diagram showing landscapes and vegetation types for the middle Late Miocene of Iceland. See Table 7.2 for species composition of vegetation types

Calycanthaceae and *Myrica* may have grown in such narrow strips of temporally-flooded lake margins. Well-drained areas at some distance from the lake were probably occupied by moderately species-rich broadleaved deciduous forests with a small proportion of conifers and evergreen shrubs in the understorey (*Rhododendron*, *Ilex*). Main trees were *Fagus gussonii, Acer* spp., *Betula,* cf. *Carpinus*, and *Ulmus*. *Fagus gussonii* is by far the most abundant element among the macrofossils, represented by leaves, bud scales, cupules, and nuts. This species is also the most abundant in the pollen record. This evidence points to an autochthonous origin of these fossils. In contrast, not a single leaf of *Quercus* has ever been recovered from the 9 to 8 Ma sediments. At the same time, *Quercus* is among the most common elements in the pollen record. This pattern may suggest that slopes facing different directions and/or having different microclimates sustained different variants of broadleaved deciduous forests. *Fagus* dominated forests would have been on the slopes facing the caldera lake (Fig. 7.4), whereas *Quercus* probably inhabited areas behind the mountain ridge surrounding the caldera lake (Fig. 7.5). Similarly, *Fagus* is typical of shady slopes in temperate regions of Central Europe, while deciduous species of *Quercus* are found on more sun-exposed slopes (Ellenberg 1986). Well-drained foothill forests were probably fairly similar to montane forests with the exception of a higher

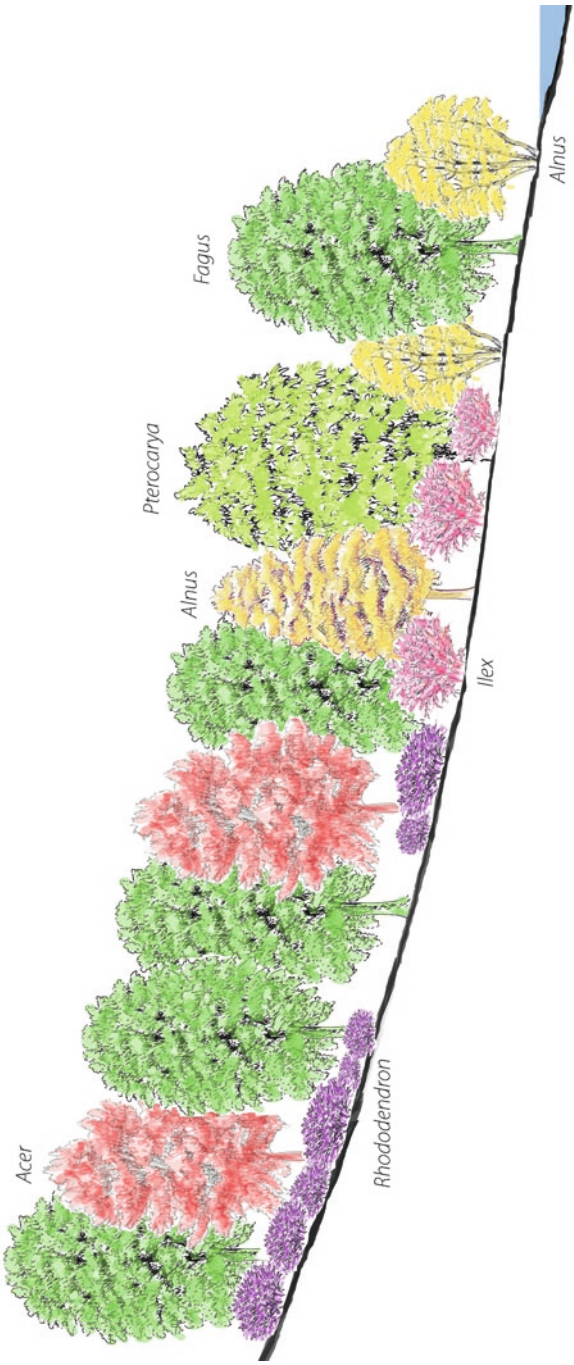



**Fig. 7.4** Schematic transect of a broadleaved deciduous forest facing the caldera lake. *Fagus gussonii* is the dominating tree species

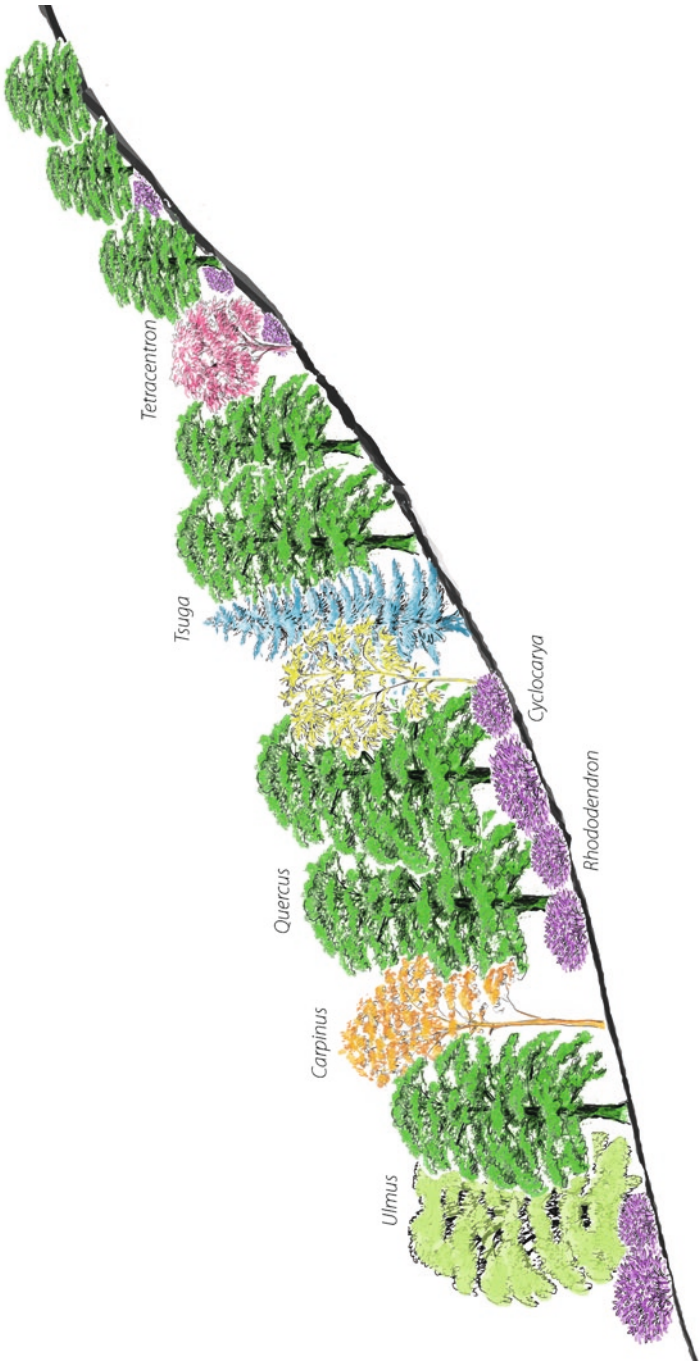



**Fig. 7.5** Schematic transect of a broadleaved deciduous forest outside the caldera. *Quercus* is the dominating tree species

proportion of conifers in the montane forests. In view of the absence of conifer taxa in the macrofossil record in the Mókollsdalur area, these montane forests may have thrived at elevations higher than the slopes surrounding the caldera. In contrast, few seeds of *Picea* have been recovered in the Skarðsströnd area (Tindafjall locality; Akhmetiev et al. 1978).

Meadow and shrubland vegetation is represented only by spore and pollen taxa, indicating they were not present in close vicinity to the caldera lake. The general scarcity of herbaceous elements in the pollen record points to a filter against pollen influx from the surrounding areas into the caldera lake, emphasizing the local character of the fossil assemblage from the 9 to 8 Ma formation.

## 7.4 Ecological and Climatic Requirements of Modern Analogues

Most of the potential modern analogues of the taxa found in the Mókolldalur area have a high climatic tolerance (Chap. 13, Appendix 13.1). In contrast, various elements that were also present in the older formations (e.g. *Ilex, Rhododendron,* and *Fagus*) require mild climatic conditions (MAT >5°C). Some taxa of the 9–8 Ma formation have been discussed in previous chapters (*Fagus, Sciadopitys,* and *Cyclocarya* in Chaps. 4, 5 and 6).

*Acer askelssonii* is similar to modern species of *Acer* sect. *Platanoidea* comprising several Eurasian species and of sect. *Acer* with a disjunct distribution in Eurasia, western and eastern North America (van Gelderen et al. 1994). Closer similarities are found with the western Eurasian species *Acer platanoides* L. (sect. *Platanoidea*) and the North American *A. saccharum* Marsh. (sect. *Acer*). *Acer platanoides* has a wide range from northern Europe to eastern and southeastern Europe, including the Caucasus, where it forms a part of the rich broadleaved deciduous forests from the lowlands to about 1,500 m a. s. l. (Hegi 1926). This species covers a wide range of climates (Cfa, Cfb, Dfb, Dfc according to Köppen; Kottek et al. 2006) with MAT 2–15°C. *Acer saccharum* has a disjunct distribution in eastern and western North America, including Mexico and Guatemala. It grows in lowlands and uplands to ca 1,000 m a. s. l. in its eastern range and up to 2,500 m a. s. l. in its western range, mainly under a Dfb climate with MAT −1.1–15.8°C (Thompson et al. 1999).

*Pterocarya* sp. from the 9 to 8 Ma formation is represented by leaves, leaflets, winged nutlets, and pollen. At present, the genus *Pterocarya* comprises six species, one in Asia Minor and five in East Asia. Two extant species are comparable to the fossil from Iceland. *Pterocarya macroptera* Batalin has winged nuts very similar to the ones recovered from the Mókollsdalur area (Grímsson et al. 2005). *Pterocarya fraxinifolia* (Lam.) Spach has leaflets with a very similar morphology to the fossil specimens.

*Pterocarya macroptera* has a large distribution from Tibet in the west to Zheijang in the east, south of 35°N (Flora of China Editorial Committee 1999). It grows in moist forests and along mountain streams in Central China, between 1,100 and

3,500 m a. s. l. The species thrives in a wide variety of climates, ranging from warm temperate ($T_{min} \geq -3°C$) to snow climates ($T_{min} < -3°C$), fully humid to winter dry, and hot to warm to cool summers (Cfa, Cfb, Cwa, Cwb, and Dwb and Dwc climate types according to Köppen; Kottek et al. 2006; Chap. 13, Table 13.1) with MAT 2.5–19.8°C. *Pterocarya fraxinifolia* is an Asian Minor species, where it typically occurs along the seashores of the Black and Caspian Seas, normally growing below 1,000 m a. s. l. In the Zagros Mountains, Iran, the species is found in altitudes up to 1,700 m a. s. l. (Akhani and Salimian 2003). *Pterocarya fraxinifolia* is an element of lowland riparian forests and of rich mixed broadleaved deciduous forests on mountain slopes. It typically thrives under a Cfa and Cfb climate (Dsa and Dsb in eastern Anatolia and the Zagros Mountains) with MAT 8.1–18.1°C (Utescher and Mosbrugger 2009). Cultivated trees flower and fruit in Scandinavia (Stockholm, MAT ca 6°C).

Pollen of *Quercus* recovered from the 9 to 8 Ma formation belongs to either *Quercus* infrageneric group *Quercus* (white oaks) or *Quercus* infrageneric group *Lobatae* (red oaks; Denk and Grimm 2010). Among modern oaks, white oaks and red oaks have the most northern and most continental distribution (Camus 1936–1938, 1938–1939, 1952–1954). Red oaks have their centre of diversity in Mexico and Central America, but some species can cope with cool temperate climates with severe winter frosts (e.g. *Q. rubra* L., MAT −1.1 to 19.4°C; Thompson et al. 1999). White oaks have a similar range as red oaks in North America, but extend further into cold continental areas (e.g. *Q. macrocarpa* Michaux, MAT −1.5 to 21.8°C, Jensen 1997; Nixon and Muller 1997; Thompson et al. 1999). In Eurasia, white oaks are clearly the most cold-tolerant members of oaks with some species (*Q. robur* L., *Q. mongolica* Fisch. ex Ledeb.) extending into areas with MAT close to the freezing point with severe frosts during the winter. *Quercus robur*, being a potential modern analogue of the fossil taxon, occurs in various climate types (mainly Cfb and Dfb according to Köppen; Kottek et al. 2006) with MAT 3.3–15°C.

Overall, a Cfb to Dfb climate can be inferred for the 9–8 Ma formation. Modern climate stations that are comparable to the middle Late Miocene of Iceland are shown in Fig. 7.6. Lowlands might have experienced milder climates with more evenly distributed precipitation (Cf climates according to Köppen; see Fig. 7.6, 2) with MAT between 8° and 10°C. In the interior, more continental conditions caused slightly lower MAT and possibly colder winters (Df climates; compare Fig. 7.6, Gothenburg, Cfb and Klagenfurt, Dfb).

## 7.5 Taxonomic Affinities and Origin of Newcomers

As in the older floras, most taxa encountered in the 9–8 Ma formation are not suggestive of particular migration routes to Iceland because they show similarities to both Eurasian and North American living and/or fossil taxa. For example, *Tsuga* comprises about nine living species in East Asia and North America. During the Tertiary, the genus was a common element in Europe and North America. A distinct type of *Tsuga* pollen occurs for the first time in the 9–8 Ma formation of Iceland. This pollen type is similar to the modern eastern North

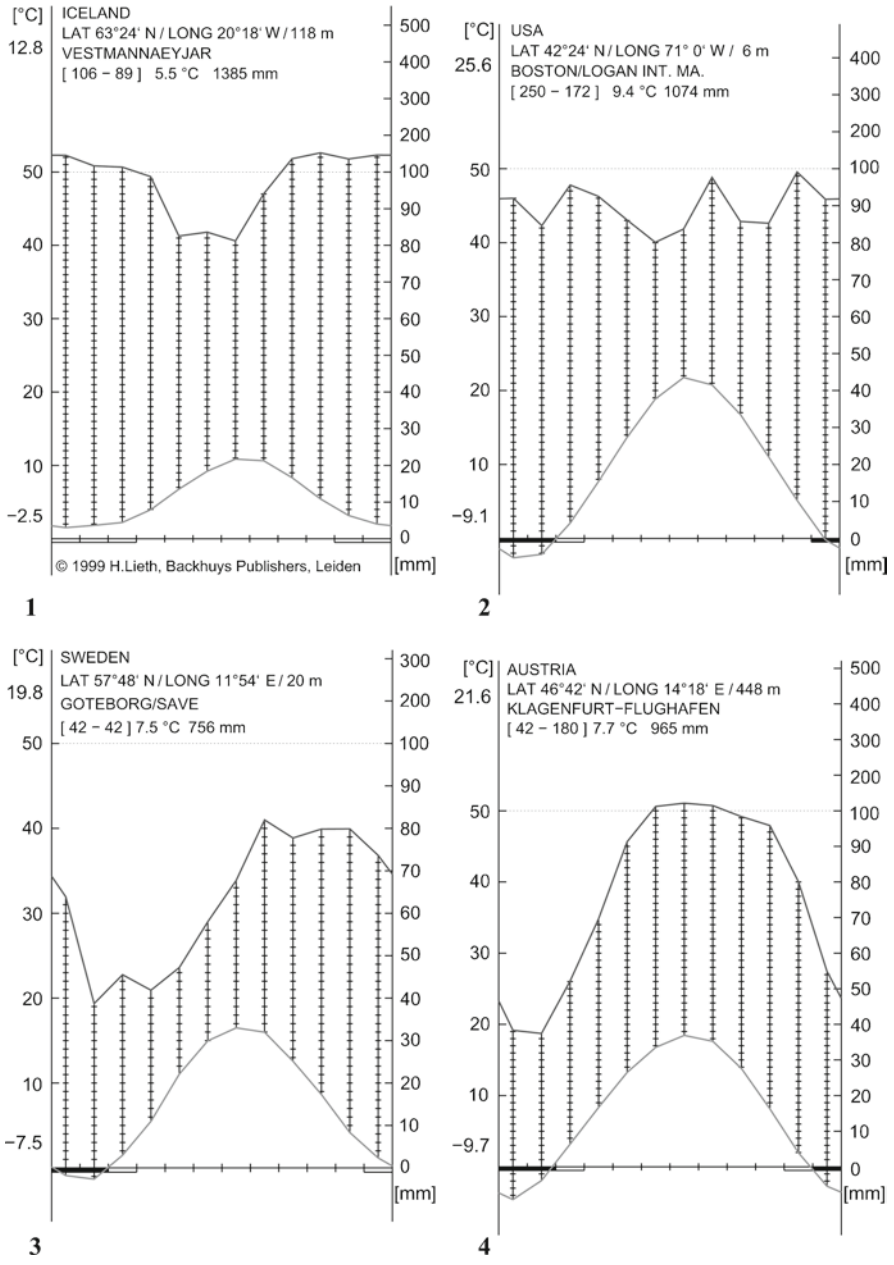



**Fig. 7.6** Climate diagrams for modern Iceland, and for climate stations resembling the climatic conditions inferred for the middle Late Miocene of Iceland (climate diagrams from Lieth et al. 1999). **1**. Vestmannaeyjar, Cfc climate. **2**. Boston, Cfb climate. **3**. Gothenburg, Cfb climate. **4**. Klagenfurt, Dfb climate (climate types according to Köppen, cf. Kottek et al. 2006)

American species *T. canadensis* (L.) Carrière (Sivak 1978). Similar types of pollen have been recovered from Tertiary sediments in Europe from the Oligocene onwards (Sivak 1978). Hence, no distinct migration route to Iceland can be determined for this taxon.

The leaves of *Betula cristata* from the Late Miocene of Iceland are comparable to another fossil taxon, *B. pseudolumnifera* Givul, a birch from the Late Miocene of southern and western Europe. The latter has been compared to the modern Japanese *B. maximowicziana* Regel (Kvaček et al. 2002). Similarities in leaf symmetry, leaf base, and dentition are also observed with the North American species *B. lenta* L. and *B. papyrifera* Marsh. According to Grímsson and Denk (2007) this taxon might have reached Iceland either from the west or from the east.

*Quercus* sp. 1 either belongs to the modern white oaks or red oaks (infrageneric groups *Quercus* and *Lobatae*, according to Denk and Grimm 2009a, 2010). While the white oaks have a northern temperate distribution, red oaks are, at present, confined to North America. Since it cannot be determined whether this pollen represents red or white oaks, it remains unclear whether it colonized Iceland from the west or from the east (Denk et al. 2010).

In contrast to the previous examples, a particular migration route to Iceland can be determined for *Fagus gussonii*. *Fagus gussonii* is a distinct Late Miocene species that has a geographical range in southern Europe and Iceland (Grímsson and Denk 2005). Although it is difficult to compare it to a particular modern species (Denk and Grimm 2009b), its Miocene distribution suggests that it migrated to Iceland from Europe. Generally, the first occurrence of oak pollen and of *Fagus gussonii* in the middle Late Miocene of Iceland strongly indicates that plants without long distance dispersal were still migrating to Iceland in this period. This in turn suggests that parts of the North Atlantic land bridge had remained subaerial until the Late Miocene (compare also Thiede and Eldholm 1983).

## 7.6 Comparison to Coeval Northern Hemispheric Floras

At the global and European scales, the time period 9–8 Ma appears not to have been characterized by dramatic shifts in climate or vegetation cover (Zachos et al. 2001; Mosbrugger et al. 2005). Northern hemispheric cooling continued gradually. In Iceland, various warmth-loving elements vanished between 10 and 9–8 Ma (e.g. *Betula islandica* [section *Costatae*], *Parthenocissus, Platanus, Smilax*). Similarly, the Homerian Stage (11.3–8 Ma) in northwestern Canada and Alaska was marked by a continuous cooling (White et al. 1997). The Grubstake flora (Alaska; Leopold and Liu 1994; Appendix 7.1) is fairly similar to the Icelandic middle Late Miocene floras. Conifers are quite diverse, including various types of *Tsuga*. Among the angiosperms, the number of temperate taxa is markedly low. *Pterocarya* occurs both in the floras of Iceland and in the Alaskan flora; *Smilax* and *Tilia* are present in the flora from Alaska but are absent in Iceland. In contrast, *Fagus* and *Ilex* are present in the Icelandic floras, while they are absent in the Grubstake flora. Herbaceous taxa play an important role both in the floras from Alaska and Iceland.

The Teewinot Formation, 8 Ma, central western USA (Barnosky 1984) is rather species-poor, containing a mixture of trees, shrubs, and herbaceous taxa. Among the Tertiary relicts are *Pterocarya, Zelkova*, and *Carya*, the records for which belong to the last ones in the Rocky Mountains. Riparian elements comprise herbaceous taxa and trees. The high percentage of *Sarcobatus* pollen found in this formation may indicate environmental conditions similar to today (BSk, steppe climate). The modern species *S. vermiculatus* (Hook.) Torr. is a halophytic shrub that occurs in western North America. *Sarcobatus*, *Ephedra*, and *Juniperus,* together with *Ulmus* and herbaceous taxa, may have inhabited drier microsites, while *Pterocarya* and *Zelkova* may have persisted in sheltered valleys (Appendix 7.1). Overall, this appears to reflect increased continentality in the Rocky Mountains in the middle Late Miocene. Older floras in western North America contain numerous elements typical of humid warm temperate vegetation types. At the same time, the extinction of humid temperate Tertiary relicts (*Pterocarya, Zelkova*) was nearly completed by 8 Ma (Barnosky 1984).

In Southern Europe, the Makrilia flora (Crete, MN11, 8.6–7.7 Ma; Sachse and Mohr 1996; Sachse 2004) is a fairly rich flora in the southeastern Mediterranean region. This flora is markedly different from co-eval high latitude floras and has a clearly subtropical appearance. Elements such as *Taxodium*, Berberidaceae, Lauraceae, Illiciaceae, Nyssaceae, evergreen oaks of *Quercus* infrageneric group *Ilex*, Rutaceae, and Symplocaceae are frequently found in the Miocene of mid-latitudes and partly span a wide stratigraphic range (Mai 1995), but reached Iceland in only a few exceptional cases (Lauraceae in the 12 Ma formation of Iceland; Chap. 5). Nevertheless, a small subset of broadleaved deciduous taxa present in the Makrilia flora is also present in the Skarðsströnd-Mókollsdalur Formation. At the generic level, this applies to *Acer, Ulmus, Carpinus, Fagus, Ilex, Pterocarya,* and *Salix* among others. Among these, members of *Acer* and *Carpinus* in the Makrilia and Mókollsdalur floras may represent quite different lineages with distinctive ecologies. Others, such as *Pterocarya* and *Fagus gussonii* may have occupied similar niches in the Mediterranean and subarctic regions at the time of deposition. *Fagus gussonii* reaches the southeasternmost limit of its distribution range in the flora of Makrilia, whereas its northwesternmost limit is in Iceland. The stenoecious nature of *Fagus* (cf. Denk and Grimm 2009b), requiring fully humid or nearly so Cf (to Df) climate types, would suggest that this taxon thrived at higher elevations on Crete (or, alternatively, the climate in Crete was remarkably humid). Given a still weaker south-north temperature gradient than today, *Fagus* would have extended to Iceland, where it grew in moist, cool temperate conditions.

## 7.7 Summary

The geological setting of the 9–8 Ma plant-bearing sedimentary rocks suggests that the plant assemblage recovered reflects regional vegetation in the vicinity of a caldera lake. The time period 9–8 Ma is characterized by impoverished broadleaved

deciduous forests. The dominant tree species were *Fagus* and possibly *Quercus*. From the Skarðsströnd-Mókollsdalur Formation, many insects have also been recovered, but they have not been studied properly with the single exception of a hickory aphid that has close biogeographic ties to eastern North America. Among plants, warmth-loving elements of the older 10 Ma formation have largely vanished. The Mókollsdalur biota shows small-scale vegetation differentiation (with slope exposure determining *Fagus*- versus *Quercus*-dominated forests) as seen in cool temperate northern hemisphere forests. Potential modern analogues of fossil taxa and vegetation types predominantly thrive under Cfb climates.

## Appendix 7.1

Floristic composition of the 9–8 Ma sedimentary formation of Iceland compared to contemporaneous northern hemispheric fossil assemblages at mid and high latitudes.

| **Skarðsströnd-Mókollsdalur flora [ca 65º30´ N 21º31´ W]** | |
|---|---|
| 9–8 Ma | |
| This study | |
| 1 | Huperzia sp. |
| 1 | Lycopodiella sp. |
| 1 | Lycopodium sp. |
| 1 | Monolete spore, fam., gen. et spec. indet. 1 |
| 1 | Monolete spore, fam., gen. et spec. indet. 2 |
| 1 | Osmunda sp. |
| 1 | Polypodiacceae gen. et spec. indet. 1 |
| 1 | Polypodiaceae gen. et spec. indet. 6 |
| 1 | Abies sp. |
| 1 | Larix sp. |
| 1 | Picea sect. Picea |
| 1 | Pinus sp. 1 |
| 1 | Pinus sp. 2 |
| 1 | Pseudotsuga sp. |
| 1 | Sciadopitys sp. |
| 1 | Tsuga sp. 1 |
| 1 | Tsuga sp. 2 |
| 1, 3 | Acer askelssonii |
| 1, 3 | Acer crenatifolium subsp. islandicum |
| 1 | aff. Calycanthaceae |
| 1, 3 | Alnus cecropiifolia |
| 3 | Angiosperm fam. et gen. indet. A |
| 1 | Apiaceae gen. et spec. indet. 1 |
| 1 | Asteraceae gen. et spec. indet. 1 |
| 1–3 | Betula cristata |
| 3 | cf. Carpinus |
| 3 | Cornus sp. |
| 3 | Cyclocarya sp. |
| 3 | Dicotylophyllum sp. D |
| 3 | Dicotylophyllum sp. E |
| 1–3 | Fagus gussonii |
| 1 | Ilex sp. 2 |
| 1 | Myrica sp. |
| 1 | Poaceae gen. et spec. indet. 1 |
| 1–3 | Pterocarya sp. |
| 1 | Quercus infrageneric group Quercus sp. 1 |
| 1 | Ranunculaceae gen. et spec. indet. 2 |
| 1 | Rhododendron sp. 2 |
| 1, 3 | Salix gruberi |
| 1 | Tetracentron atlanticum |
| 1 | Thalictrum sp. 2 |
| 1–3 | Ulmus section Ulmus sp. |

**Teewinot flora, lower Gros Ventre River [ca 43º 35´ N 110º 21´ W]**
8 Ma
Barnosky, 1984

| | |
|---|---|
| 1 | **Abies sp**. |
| 1 | Cupressaceae |
| 1 | Juniperus sp. |
| 1 | **Picea sp.** |
| 1 | **Pinus sp.** |
| 1 | Ephedra sp. |
| 1 | Artemisia sp. |
| 1 | Carya sp. |
| 1 | Chenopodiineae |
| 1 | Cyperaceae |
| 1 | Gilia sp. |
| 1 | **Gramineae [=Poaceae]** |
| 1 | **Pterocarya sp.** |
| 1 | **Salix sp.** |
| 1 | Sapindaceae sp. |
| 1 | Sarcobatus sp. |
| 1 | Sparganium sp. |
| 1 | **Tubuliflorae spp. [=Asteraceae]** |
| 1 | **Ulmus / Zelkova sp.** |

**Grubstake flora, Alaska [ca 64º N 148º 11´ E]**
8 Ma
Leopold & Liu, 1994; White et al., 1997

| | |
|---|---|
| 1 | Cyathea sp. |
| 1 | **Lycopodium cf. L. alopecuroides** |
| 1 | **Lycopodium cf. L. annotinum** |
| 1 | **Lycopodium cf. L. complanatum** |
| 1 | **Lycopodium cf. L. lucidulum** |
| 1 | **Osmunda sp.** |
| 1 | Selaginella sp. |
| 1 | Abies cf. A. grandis |
| 1 | **Larix / Pseudotsuga sp.** |
| 1 | **Picea sp.** |
| 1 | **Pinus spp.** |
| 1 | **Tsuga cf. T. canadensis** |
| 1 | **Tsuga cf. T. heterophylla** |
| 1 | **Tsuga cf. T. mertensiana** |
| 1 | **Alnus cf. firma** |
| 1 | **Alnus spp.** |
| 1 | Araliaceae |
| 1 | **Betula sp.** |
| 1 | Caprifoliaceae |
| 1 | ?Castanea / Castanopsis sp. – *reworked grains* |
| 1 | **Chenopodiaceae** |
| 1 | **Chenopodiineae** |
| 1 | Corylus sp. |
| 1 | **Cyperaceae** |
| 1 | ?Diervilla / Weigela sp. |
| 1 | **Ericales** |
| 1 | **Gramineae [=Poaceae]** |
| 1 | Juglans sp. |
| 1 | Juncus sp. |
| 1 | ?Magnolia sp. – *reworked grains* |
| 1 | **Myrica sp.** |
| 1 | Onagraceae |
| 1 | Polygonum persicaria |
| 1 | **Pterocarya sp.** |
| 1 | **Ranunculaceae** |
| 1 | **Rhododendron sp.** |
| 1 | **Salix sp.** |
| 1 | Smilax sp. |
| 1 | Sparganium sp. |
| 1 | Tilia sp. |
| 1 | Typha sp. |
| 1 | **Ulmus/Zelkova sp.** |
| 1 | Viburnum sp. |

**Makrilia flora, Crete [ca 35°03´ N 25°43´ E]**
8.6–7.7 Ma
Sachse & Mohr, 1996; Sachse, 2004

| | |
|---|---|
| 1 | **Abies sp.** |
| 1 | Cathaya sp. |
| 1 | Cedrus sp. |
| 1 | Cupressaceae |
| 1 | **Picea sp.** |
| 1, 2 | **Pinaceae** |
| 2 | **Pinidae** |
| 1, 3 | **Pinus cf. hampeana** |
| 1, 3 | **Pinus cf. hepios** |
| 1, 3 | **Pinus spp.** |
| 1, 3 | Tetraclinis salicornoides |
| 1, 3 | Tetraclinis sp. |
| 1, 3 | Taxodium dubium |
| 1 | **Tsuga sp.** |
| 1 | Ephedra sp. |
| 3 | **Acer decipiens** |
| 1, 2 | **Acer spp.** |

(continued)

**Makrilia flora** (continued)

| | |
|---|---|
| 1, 2 | **aff. Ulmus sp.** |
| 2 | Ailanthus vel Chenopodiaceae |
| 1, 3 | **Alnus sp.** |
| 3 | Ampelopsis vel Vitis |
| 1 | Apiaceae |
| 1 | **Aquifoliaceae** |
| 1, 2 | Aquilaria sp. |
| 1 | Araliaceae |
| 1 | **Asteraceae** |
| 1 | **Asteroideae** |
| 3 | Berberis/Mahonia sp. |
| 1 | Brassiacaceae |
| 1 | Buxus cf. bahamensis |
| 1, 3 | Buxus cf. egeriana |
| 1, 3 | Buxus pliocenica |
| 1, 3 | **Carpinu sp.** |
| 1, 2 | **Carpinus cf. orientalis** |
| 1, 2 | Carya sp. |
| 1 | Caryophyllaceae |
| 1 | Celastraceae |
| 1 | Celastrus sp. |
| 1 | Celtis sp. |
| 1 | cf. Centaurea |
| 1 | Chenopodiaceae |
| 3 | Cinnamomophyllum sp. |
| 1 | Cistus sp. |
| 3 | Cladastris sp. |
| 1 | Convolvulus spp. |
| 3 | Cymodocea vel Posidonia |
| 1, 3 | Cyperaceae |
| 1 | cf. Cyrilla sp. |
| 3 | cf. Dalbergia sp. |
| 1 | Dipcadi sp. |
| 1–3 | Engelhardieae |
| 1 | Ericaceae vel Empetraceae |
| 1, 3 | Ericaceae vel Myrtaceae |
| 1, 3 | **Fagus cf. attenuata** |
| 3 | **Fagus cf. gussonii** |
| 2 | Fraxinus sp. |
| 1 | Hedera |
| 1 | Helianthemum sp. |
| 2 | Homalium vel Styracaceae |
| 1, 3 | **Ilex cf. aquifolium** |
| 3 | Illicium rhenanum |
| 1 | Juglans sp. |
| 1 | Lamiaceae |
| 3 | Laurophyllum spp. |
| 1 | Leea sp. |
| 1–3 | Leguminosae spp. |
| 2, 3 | cf. Leguminosites spp. |
| 1 | Liliaceae |
| 1 | Linum spp. |
| 1, 3 | Lonicera cf. etrusca |
| 3 | Machaerium spp. |
| 3 | Magnolia sp. |
| 1 | Microtropis cf. fallax |
| 1 | Molospermum sp. |
| 3 | Monocotyledonae |
| 1 | Morus cf. nigra |
| 1, 3 | Myrica cf. lignitum |
| 1 | Myristicaceae |
| 3 | Myrtaceae |
| 1 | Nypa |
| 1 | Nyssaceae |
| 1 | Oleaceae |
| 1 | cf. Peristophe sp. |
| 3 | Phillyrea sp. |
| 3 | Pistacia cf. lentiscus |
| 1 | Plantaginaceae |
| 1 | **Poaceae** |
| 1 | Polygonaceae |
| 2 | Populus sp. |
| 1 | Potamogeton cf. lucens |
| 1 | Potamogeton sp. |
| 1 | **Pterocarya sp.** |
| 1, 3 | **Quercus cf. mediterranea** |
| 1, 3 | **Quercus kubinyi** |
| 1, 3 | **cf. Quercus rhenana** |
| 1, 2 | **Quercus spp.** |
| 1, 2 | **Ranunculaceae** |
| 2 | cf. Ruppia sp. |
| 1 | Ruta/Dictamus sp. |
| 3 | **Salix cf. purpurea** |
| 1, 3 | **Salix spp.** |
| 1 | Sambucus sp. |
| 1 | Sanguisorba sp. |
| 1 | Sapotaceae |
| 3 | cf. Smilax sp. |
| 1 | Sparganiaceae |
| 3 | Swartzia sp. |
| 3 | Symplocos cf. minutula |
| 1 | Symplocos sp. |
| 1, 2 | Tilia sp. |
| 1 | Tiliaceae |
| 2 | cf. Toddalia sp. |

(continued)

| | |
|---|---|
| **Makrilia flora** (continued) | |
| 1 | Typha sp. |
| 3 | **Ulmus plurinerva** |
| 1 | Zelkova davidii |
| 1, 3 | Zelkova zelkovaefolia |

Boldface indicates that genus is present in the Skarðsströnd-Mókollsdalur Formation. Grey shading indicates that genus is present in younger and older formations in Iceland. *1* based on pollen, spores; *2* based on leaves and/or fruit/seed fossils; *3* based on leaf fossils

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## Explanation of Plates

**Plate 7.1** **1**. Hrútagil in Mókollsdalur, northwestern Iceland, Skarðsströnd-Mókollsdalur Formation (ca 8 Ma). Stream running down the Hrútagil gully, outcrop with fossils in middle of photo, Mókollsdalur valley seen in the background. **2**. View up the gully Hrútagil from Mókollsdalur valley. **3–7**. Variation in preservation of plant fossils and sedimentary rock type (diatomite, siltstone, sandstone). Most fossils are preserved as compressions with some organic material on both part and counterpart, but some only as impressions

**Plate 7.2** **1–3**. *Lycopodiella* sp. **1**. Spore in SEM, proximal polar view showing trilete tetrad mark. **2**. Detail of spore surface. **3**. Spore in LM, proximal polar view showing trilete tetrad mark. **4–6**. *Lycopodiella* sp. **4**. Spore in SEM, proximal polar view. **5**. Detail of spore surface. **6**. Spore in LM, distal polar view. **7–9**. Lycopodium sp. **7**. Spore in SEM. **8**. Detail of spore surface. **9**. Spore in LM. **10–12**. Lycopodium sp. **10**. Spore in SEM, distal polar view. **11**. Detail of spore surface. **12**. Spore in LM, polar view

**Plate 7.3** **1–3**. *Huperzia* sp. **1**. Spore in SEM, distal polar view. **2**. Detail of spore surface. **3**. Spore in LM, proximal polar view showing trilete tetrad mark. **4–6**. *Osmunda* sp. **4**. Spore in SEM, oblique polar view. **5**. Detail of spore surface. **6**. Spore in LM, oblique polar view. **7–9**. *Osmunda* sp. **7**. Spore in SEM. **8**. Detail of spore surface. **9**. Spore in LM. **10–12**. Polypodiaceae gen. et spec. indet. 1. **10**. Monolete spore in SEM, equatorial view. **11**. Detail of spore surface. **12**. Spore in LM, equatorial view

**Plate 7.4** **1–3**. Polypodiaceae gen. et spec. indet. 6. **1**. Spore in SEM, distal polar view. **2**. Detail of spore surface. **3**. Spore in LM, polar view. **4–6**. Monolete spore fam. gen. et spec. indet. 1. **4**. Spore in SEM, proximal polar view showing monolete tetrad mark. **5**. Detail of spore surface. **6**. Spore in LM. **7–9**. Monolete spore fam. gen. et spec. indet. 2. **7**. Spore in SEM, proximal polar view showing monolete tetrad mark. **8**. Detail of spore surface. **9**. Spore in LM, oblique polar view. **10–12**. Monolete spore fam. gen. et spec. indet. 2. **10**. Spore in SEM, distal polar view. **11**. Detail of spore surface. **12**. Spore in LM, proximal polar view showing monolete tetrad mark

**Plate 7.5** **1–3**. Larix/Pseudotsuga sp. **1**. Pollen grain in SEM. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM. **4**. Picea sp., winged seed (IMNH org 147). **5–7**. Picea sp. **5**. Bisaccate pollen grain in SEM, equatorial view. 6. Detail of cappa surface. **7**. Bisaccate pollen grain in LM, equatorial view. **8–11**. Pinus sp. 2 (Diploxylon type). **8**. Bisaccate pollen grain in SEM, equatorial view. **9**. Detail of cappa surface. **10**. Bisaccate pollen grain in LM, polar view. **11**. Bisaccate pollen grain in LM, equatorial view

**Plate 7.6** **1–3**. *Pinus* sp. 2 (Haploxylon type). **1**. Bisaccate pollen grain in SEM, equatorial view. **2**. Detail of cappa surface. **3**. Bisaccate pollen grain in LM, equatorial view. **4–6**. *Larix/Pseudotsuga* sp. **4**. Pollen grain in SEM. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM. **7–9**. *Sciadopitys* sp. **7**. Pollen grain in SEM, distal polar view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM

**Plate 7.7** **1–4**. *Tsuga* sp.1 **1**. Monosaccate pollen grain in SEM, distal polar view. **2**. Monosaccate pollen grain in LM, distal polar view. **3**. Detail of saccus. **4**. Detail of corpus. **5–8**. *Tsuga* sp. 2. **5**. Monosaccate pollen grain in SEM, distal polar view. **6**. Monosaccate pollen grain in LM, distal polar view. **7**. Detail of saccus. **8**. Detail of corpus

**Plate 7.8** **1–3**. Apiaceae gen. et spec. indet. 5. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4–6**. Apiaceae gen. et spec. indet. 1. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7–9**. *Ilex* sp. 2. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view. **10–12**. Asteraceae gen. et spec. indet. 1. **10**. Pollen grain in SEM, polar view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, polar view

**Plate 7.9** **1**. *Alnus cecropiifolia*, large wide elliptic leaf (IMNH). **2**. Detail of Fig. 1 showing tertiary venation and teeth along margin. **3**. *Alnus cecropiifolia*, large elliptic leaf (IMNH). **4**. *Alnus kefersteinii*, female infructescences (IMNH). **5**. *Alnus kefersteinii*, female infructescences (IMNH). **6**. *Alnus/Betula* sp., male catkins (IMNH). **7–9**. *Alnus* sp. 1. **7**. Detail of pollen grain surface. **8**. Pollen grain in SEM, polar view. **9**. Pollen grain in LM, polar view

**Plate 7.10** **1.** *Betula cristata*, large ovate leaf (IMNH). **2.** *Betula cristata*, large ovate leaf (IMNH). **3.** *Betula cristata*, catkin scale (IMNH). **4.** *Betula cristata*, small narrow elliptic leaf. **5–7.** *Betula* sp. **5.** Pollen grain in SEM, polar view. **6.** Detail of pollen grain surface. **7.** Pollen grain in LM, polar view

**Plate 7.11** **1.** cf. *Carpinus* sp., narrow elliptic leaf with cordate base, numerous small teeth along margin (IMNH org 149). **2.** *Cornus* sp., wide elliptic leaf, entire margined (IMNH). **3–5.** aff. Calycanthaceae **3.** Pollen grain in SEM, equatorial view. **4.** Detail of pollen grain surface. **5.** Pollen grain in LM, equatorial view

**Plate 7.12** **1–4.** *Rhododendron* sp. 2. **1.** Tetrad in SEM. **2.** Tetrad in LM. **3.** Detail of tetrad surface close to apertures. **4.** Detail of tetrad surface in mesocolpium. **5–7.** *Fagus* sp. (*F. gussonii*). **5.** Pollen grain in SEM, oblique equatorial view. **6.** Detail of pollen grain surface. **7.** Pollen grain in LM, oblique equatorial view. **8–10.** *Fagus* sp. (*F. gussonii*). **8.** Pollen grain in SEM, polar view. **9.** Detail of pollen grain surface. **10.** Pollen grain in LM, polar view

**Plate 7.13** **1–4.** *Fagus gussonii*. **1.** Medium sized leaf with oblong base with obtuse very-base (IMNH). **2.** Part of leaf, medium sized wide elliptic. **3.** Medium sized elliptic leaf with dentate margin and acuminate apex (IMNH). **4.** Large elliptic leaf with obtuse base, weakly dentate margin (IMNH)

**Plate 7.14 1–10.** *Fagus gussonii*. **1.** Medium sized elliptic leaf with obtuse base and craspedodromous venation (IMNH). **2.** Small leaf with dentate margin (IMNH). **3**. Cupule with a long peduncle (IMNH). **4.** Cupule with part of peduncle (IMNH). **5.** Cupule with traces of spine-like appendages (IMNH). **6.** Bud scale (IMNH). **7.** Bud scale (IMNH). **8.** Bud scale (IMNH). **9.** Winged nut (IMNH). **10.** Winged nut (IMNH). **11–13.** *Quercus* infrageneric group *Quercus* sp. 1. **11.** Pollen grain in SEM, equatorial view. **12.** Detail of pollen grain surface. **13.** Pollen grain in LM, equatorial view

**Plate 7.15 1.** *Pterocarya* sp., compound leaf (IMNH org 72). **2.** *Pterocarya* sp., large leaflet (IMNH). **3.** *Pterocarya* sp., nutlet with two lateral wings (IMNH org 73). **4.** Detail of Fig. 2 showing teeth along margin. **5.** Detail of Fig. 2 showing asymmetric base. **6.** *Cyclocarya* sp., large leaflet (IMNH)

**Plate 7.16 1–3**. *Pterocarya* sp. **1.** Pollen grain in SEM, polar view. **2.** Detail of pollen grain surface. **3.** Pollen grain in LM, polar view. **4–6.** *Pterocarya* sp. **4.** Pollen grain in SEM, polar view. **5.** Detail of pollen grain surface. **6.** Pollen grain in LM, polar view. **7–9.** *Myrica* sp. **7.** Pollen grain in SEM, polar view. **8.** Detail of pollen grain surface. **9.** Pollen grain in LM, polar view. **10–12.** *Myrica* sp. **10.** Pollen grain in SEM, polar view. **11.** Detail of pollen grain surface. **12.** Pollen in LM, polar view

**Plate 7.17 1–3.** Poaceae gen. et spec. indet. 1. **2.** Pollen grain in SEM. **2.** Detail of pollen grain surface. **3.** Pollen grain in LM. **4–6.** *Thalictrum* sp. 2. **4.** Pollen grain in SEM. **5.** Detail of pollen grain surface. **6.** Pollen grain in LM. **7–9.** Ranunculaceae gen. et spec. indet. 2. **7.** Pollen grain in SEM, equatorial view. **8.** Detail of pollen grain surface. **9.** Pollen grain in LM, equatorial view. **10–12.** Ranunculaceae gen. et spec. indet. 2. **10.** Pollen grain in SEM, equatorial view. **11.** Detail of pollen grain surface. **12.** Pollen grain in LM, equatorial view

**Plate 7.18 1.** *Salix gruberi*, part of leaf (IMNH). **2.** *Acer askelssonii*, large 7 lobed leaf (IMNH). **3.** *Acer askelssonii*, large 5 lobed leaf (IMNH)

**Plate 7.19 1.** *Acer crenatifolium* subsp. *islandicum*, small narrow 3 lobed leaf (IMNH). **2.** *Acer crenatifolium* subsp. *islandicum*, medium sized 3 lobed leaf (IMNH). **3.** Detail of Fig. 2 showing venation between lobes

**Plate 7.20 1–3.** *Acer* sp.1. **1.** Pollen grain in SEM, equatorial view. **2.** Detail of pollen grain surface. **3.** Pollen grain in LM, equatorial view. **4–6.** *Acer* sp.1. **4.** Pollen grain in SEM, equatorial view. **5.** Detail of pollen grain surface. **6.** Pollen grain in LM, equatorial view. **7–9.** *Acer* sp. 1. **7.** Pollen grain in SEM, equatorial view. **8.** Detail of pollen grain surface. **9.** Pollen grain in LM, equatorial view. **10–12.** *Acer* sp. 2. Pollen grain in SEM, equatorial view. **11.** Detail of pollen grain surface. **12.** Pollen grain in LM, equatorial view

**Plate 7.21 1–3.** *Tetracentron atlanticum*. **1.** Pollen grain in SEM, polar view. **2.** Detail of pollen grain surface. **3.** Pollen grain in LM, polar view. **4–6.** *Tetracentron atlanticum*. **4.** Pollen grain in SEM, equatorial view. **5.** Detail of pollen grain surface. **6.** Pollen grain in LM, equatorial view. **7–9.** *Ulmus* sp. **7.** Pollen grain in SEM, oblique view. **8.** Detail of pollen grain surface. **9.** Pollen grain in LM, polar view. **10–12.** *Ulmus* sp. **10.** Pollen grain in SEM, polar view. **11.** Detail of pollen grain surface. **12.** Pollen grain in LM, polar view

**Plate 7.22 1.** *Ulmus* sp. MT 2, medium sized elliptic leaf (IMNH 4742-02). **2.** *Ulmus* sp. MT 2, small elliptic leaf (IMNH 4742-01). **3.** *Ulmus* section *Ulmus* sp., samara, endocarp with wing (IMNH). **4.** Detail of Fig. 3 showing apical notch of wing

**Plate 7.23 1–4.** Angiosperm fam. gen. et spec. indet A. **5.** *Dicotylophyllum* sp. D, seedling with leaves (IMNH 5561). **6.** *Dicotylophyllum* sp. E, leaf or leaflet (IMNH)

# Plates




**Plate 7.1**

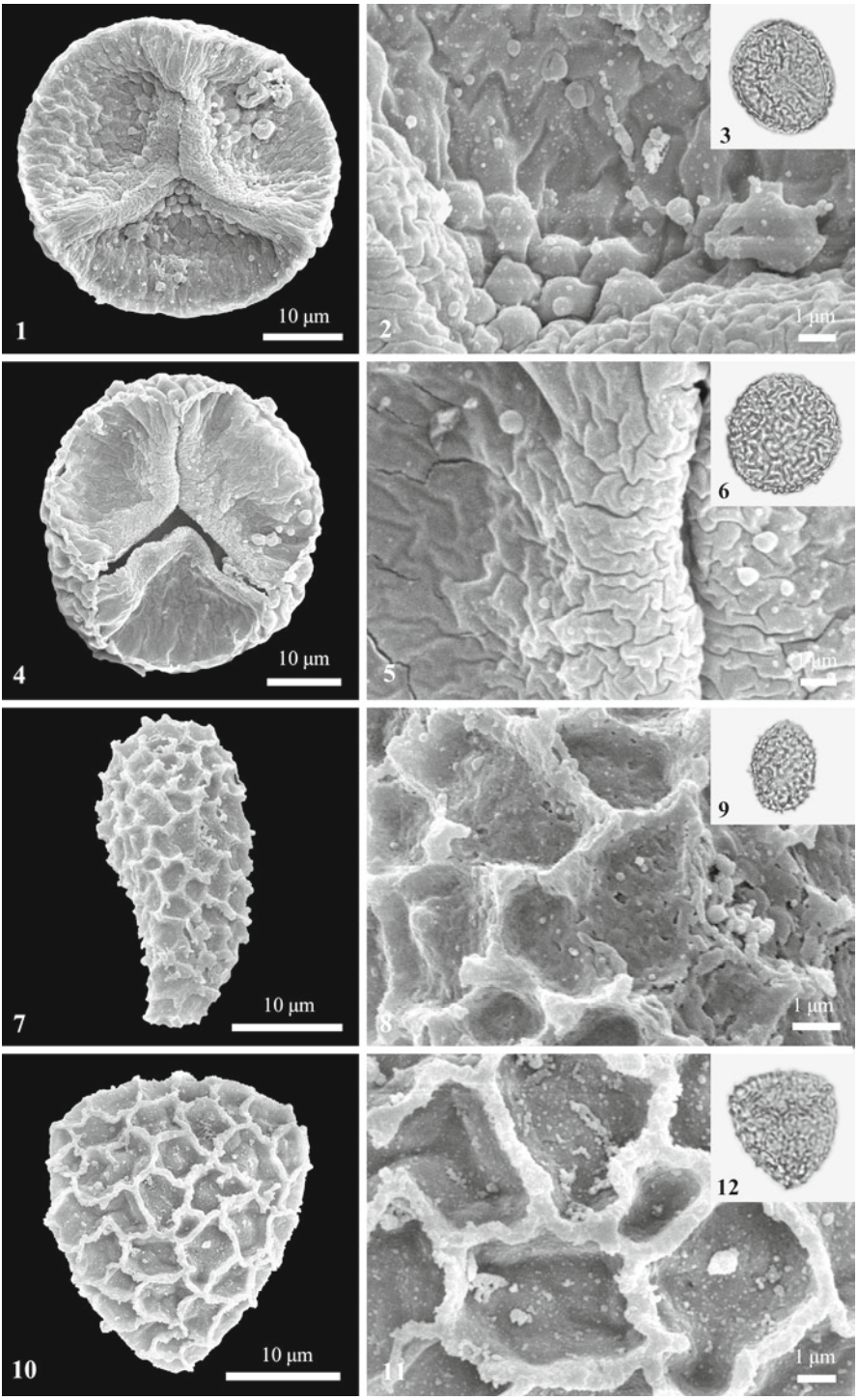



**Plate 7.2**

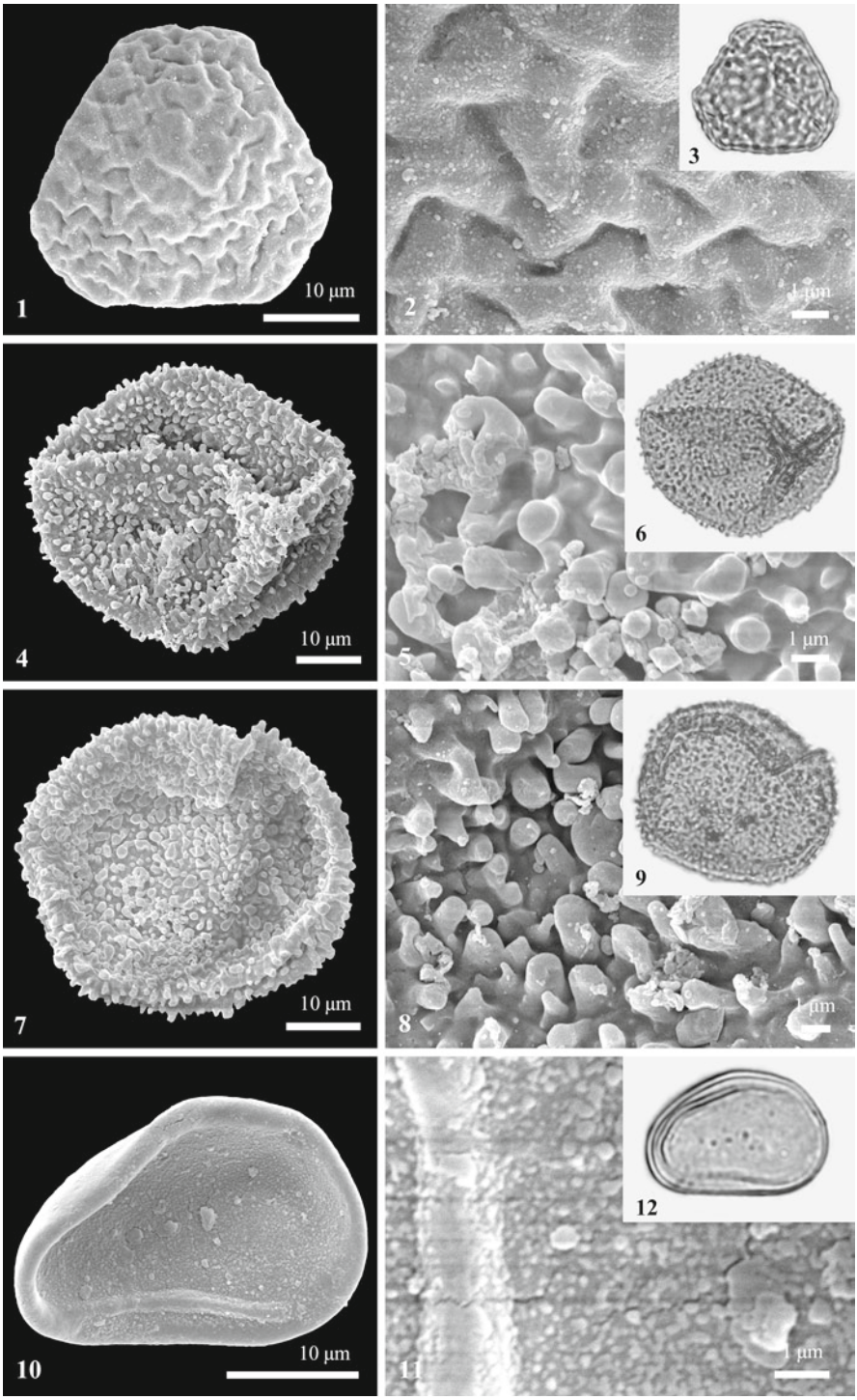



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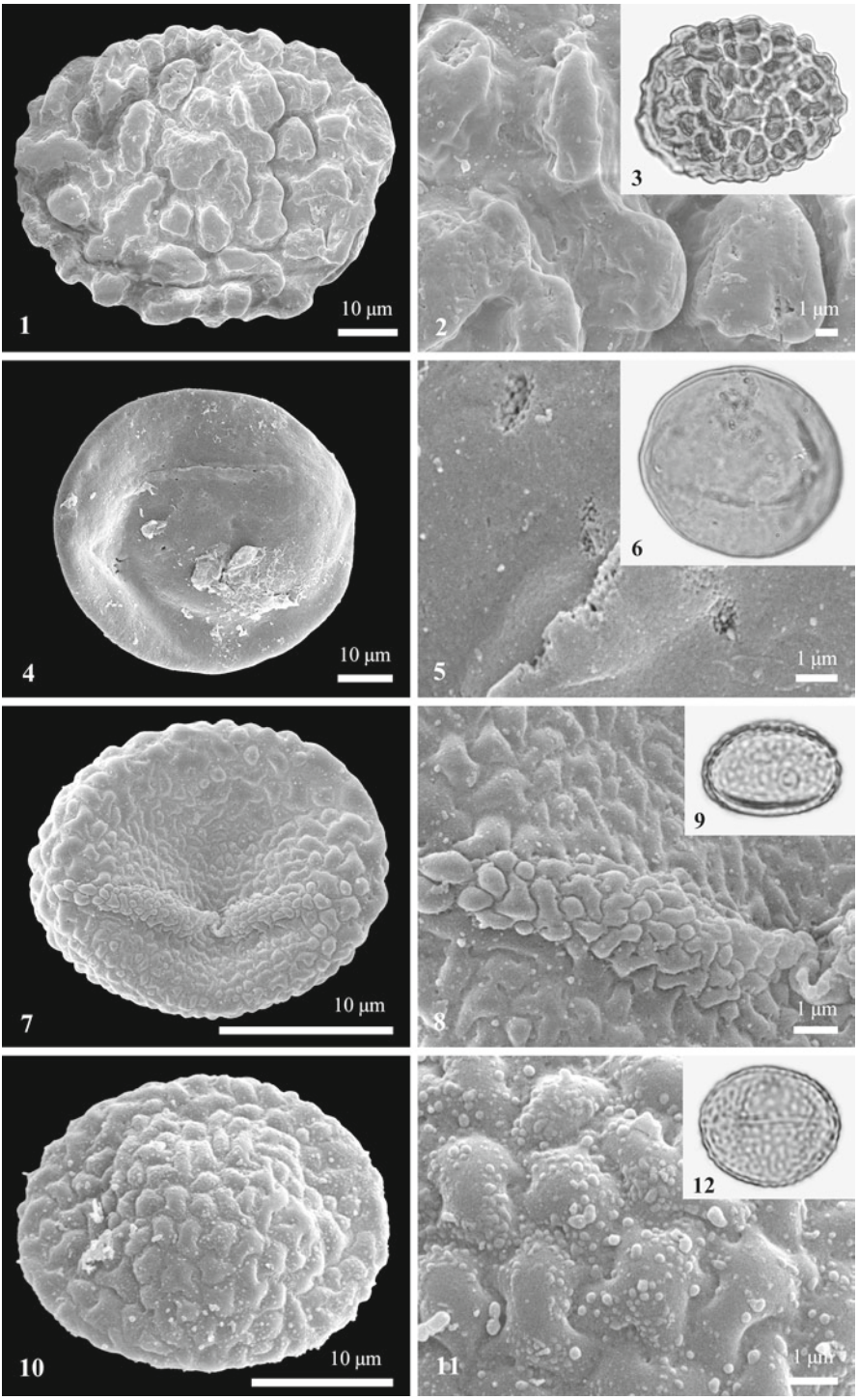



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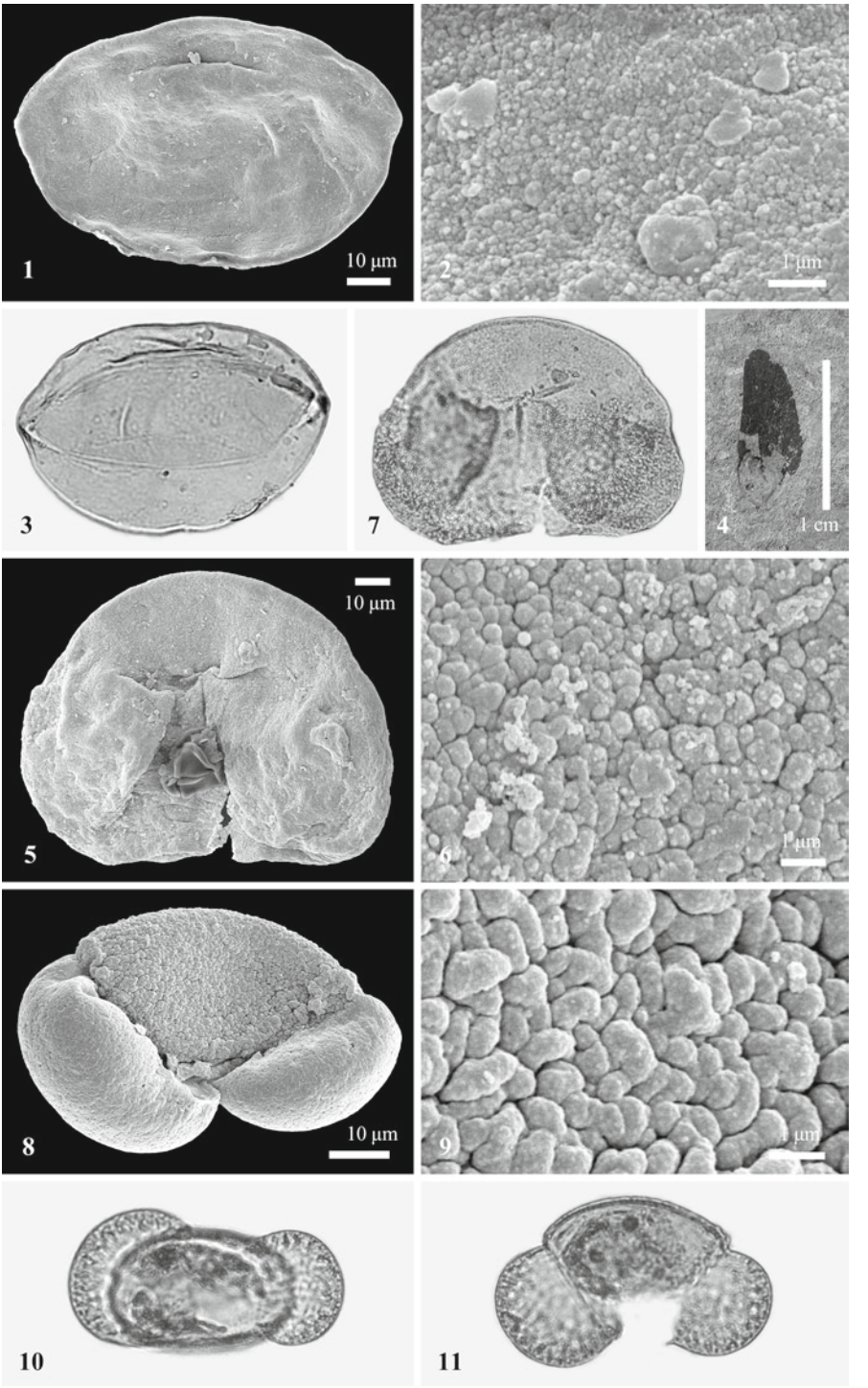



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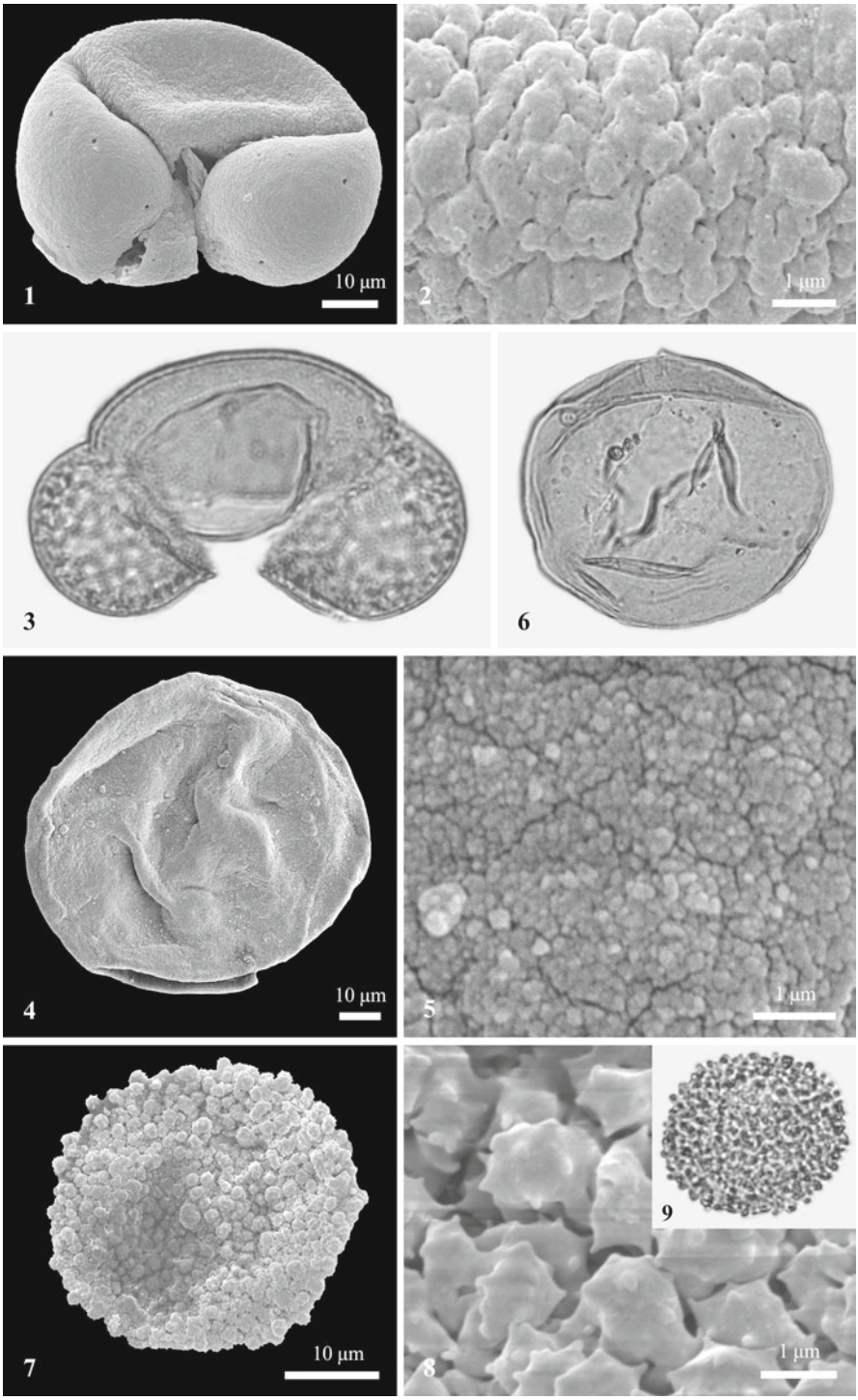



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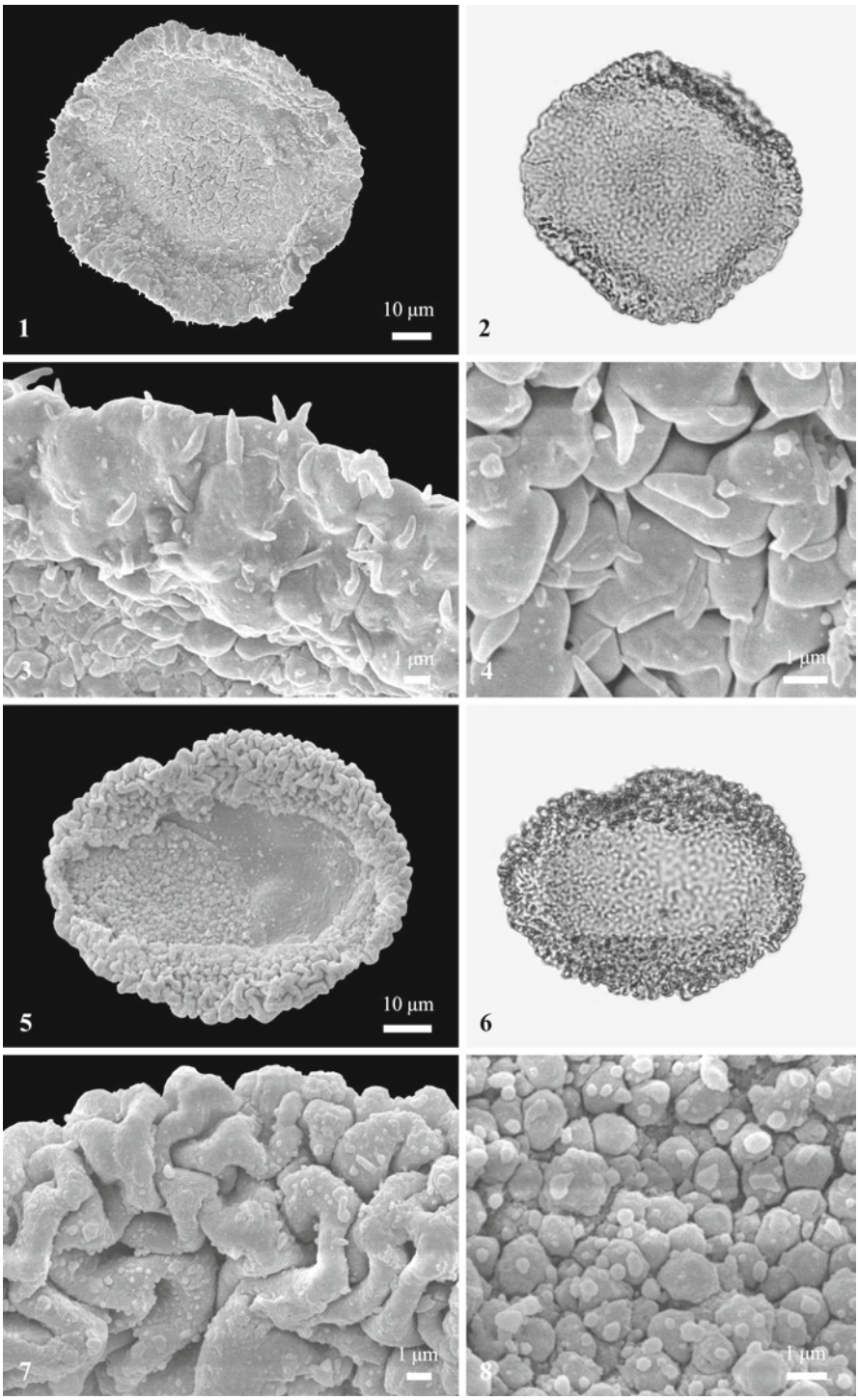



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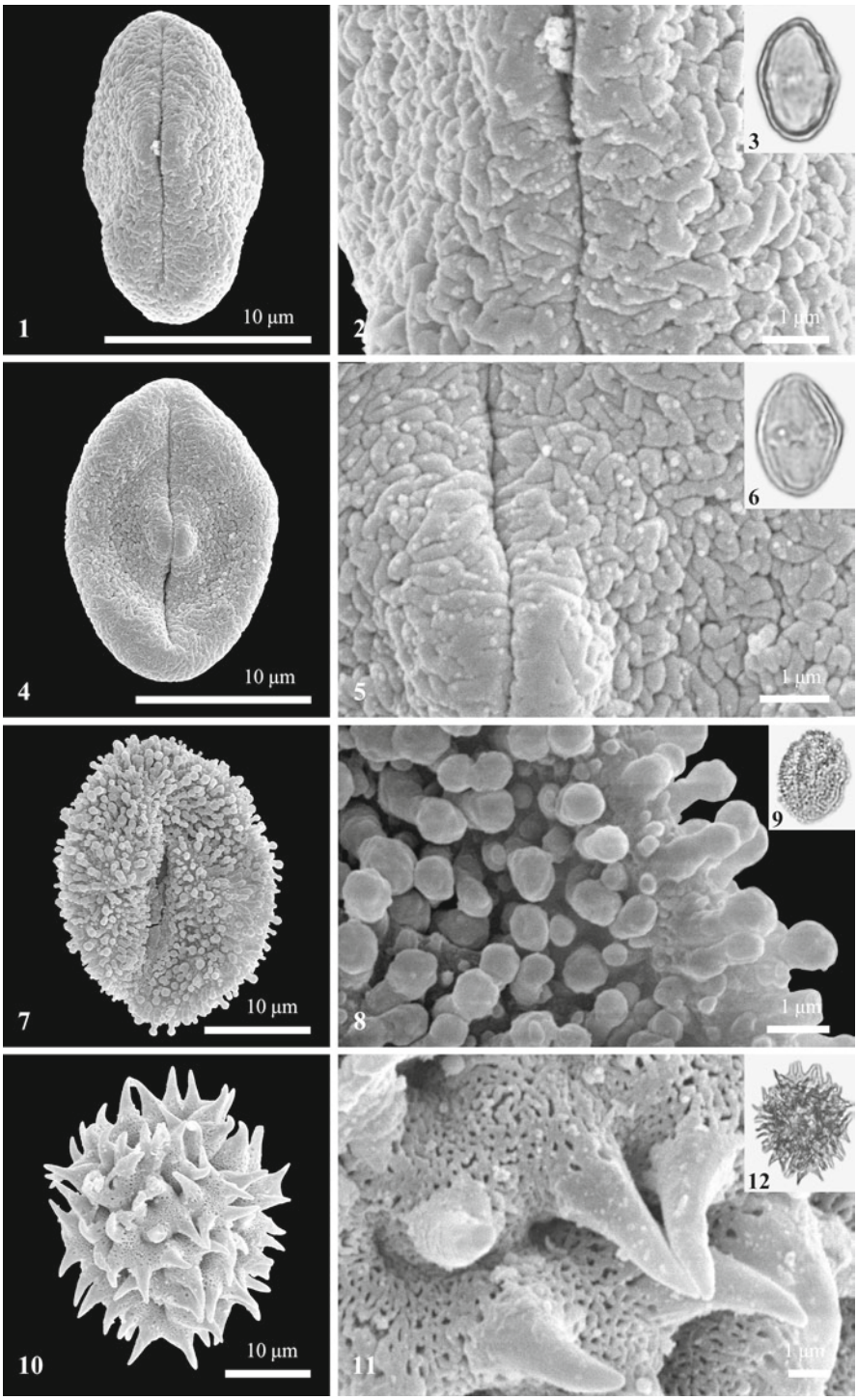



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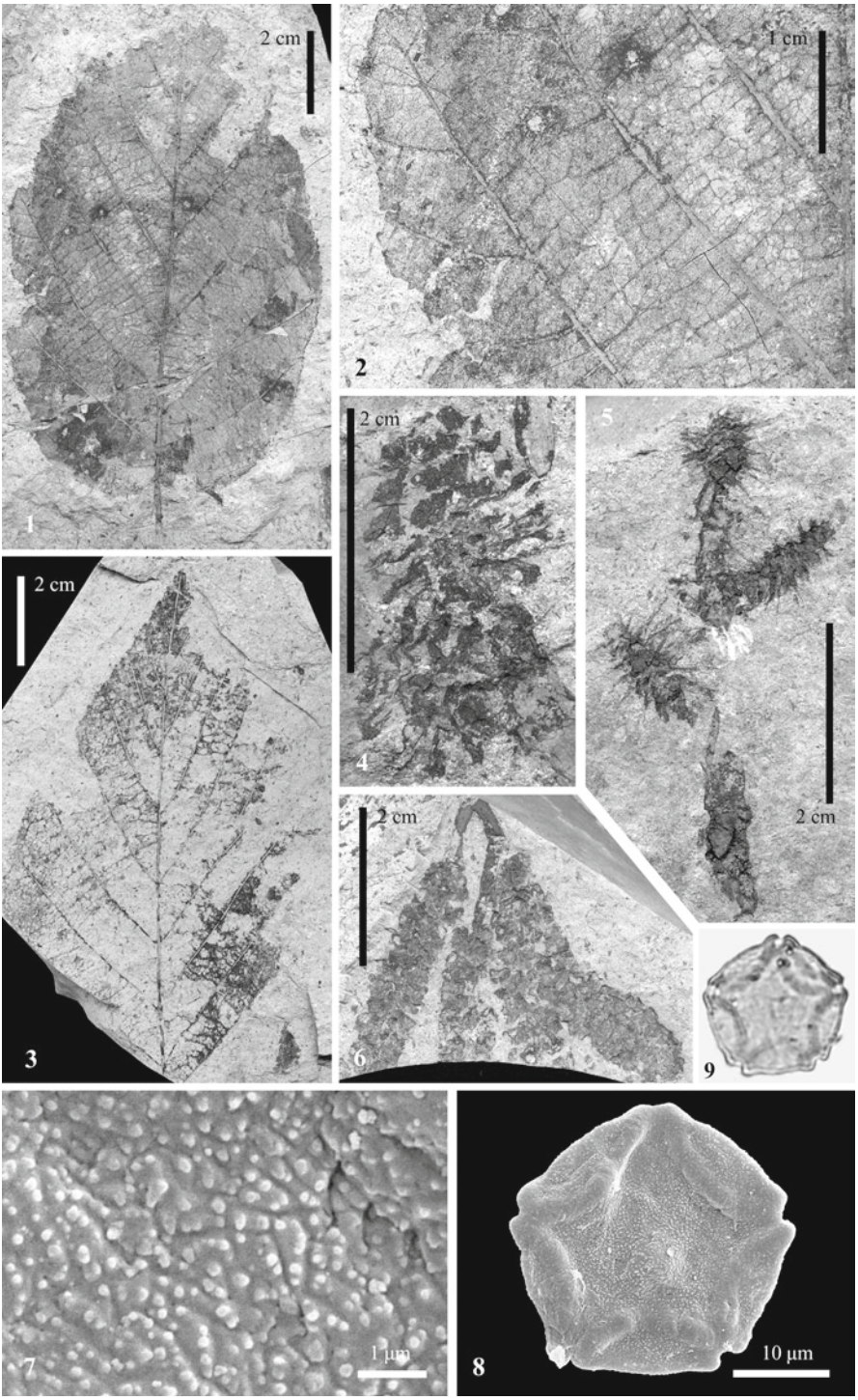



**Plate 7.9**

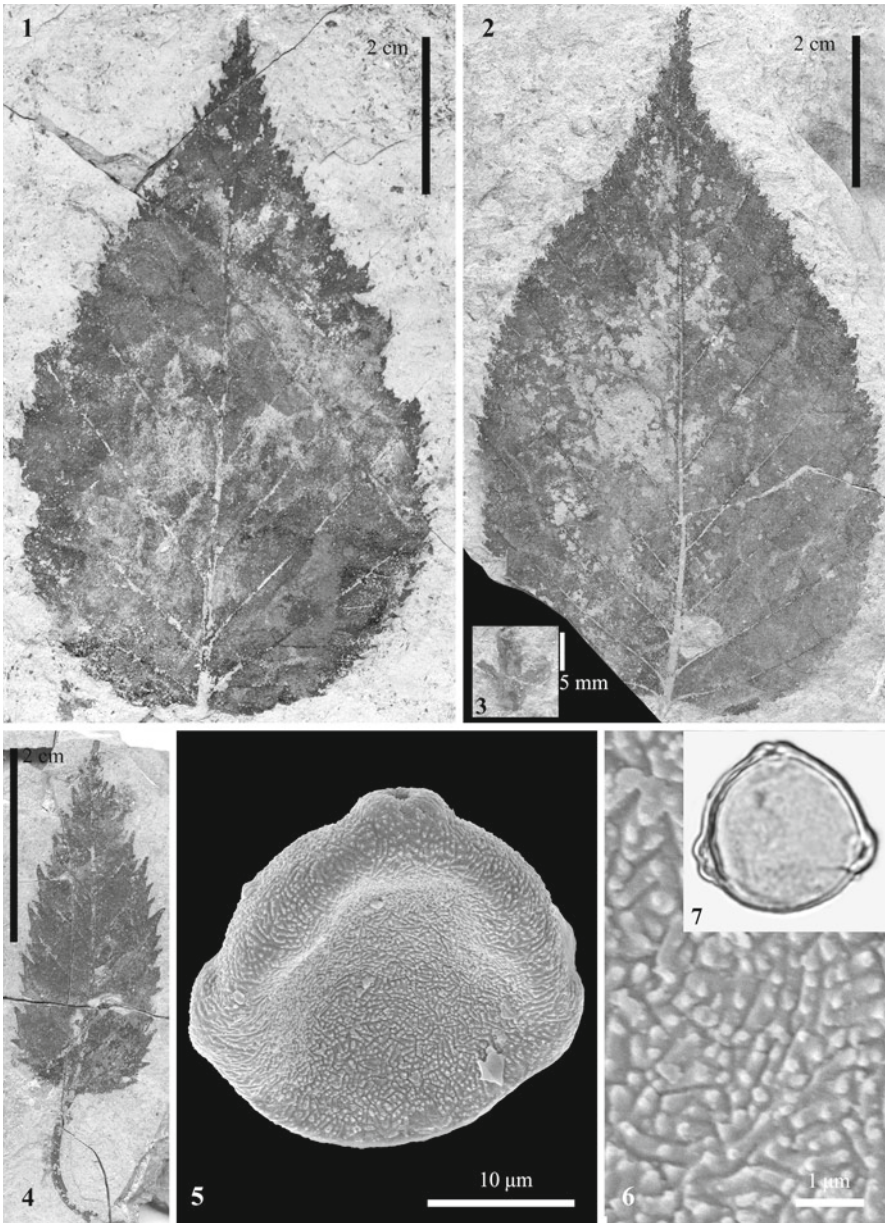



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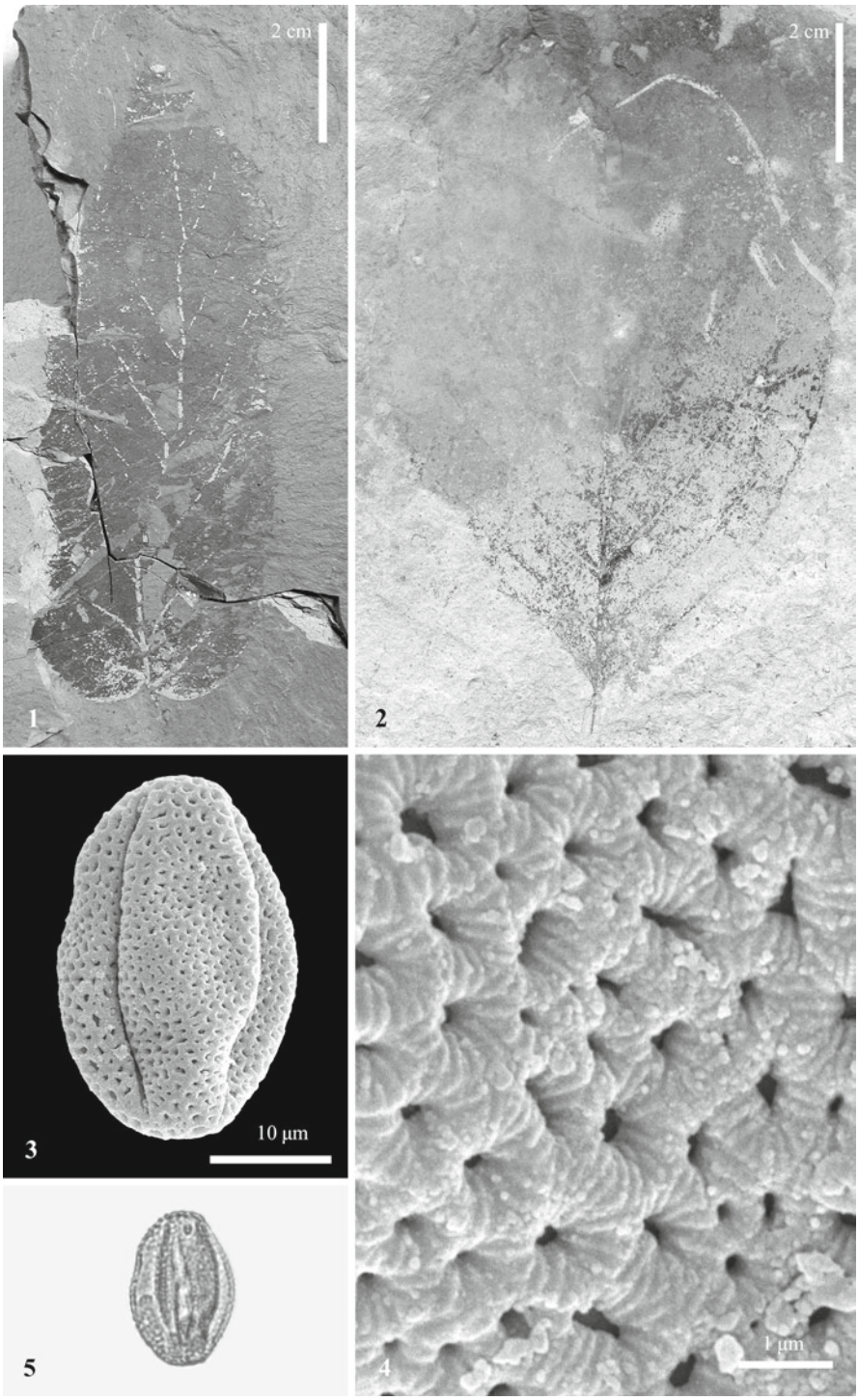



**Plate 7.11**

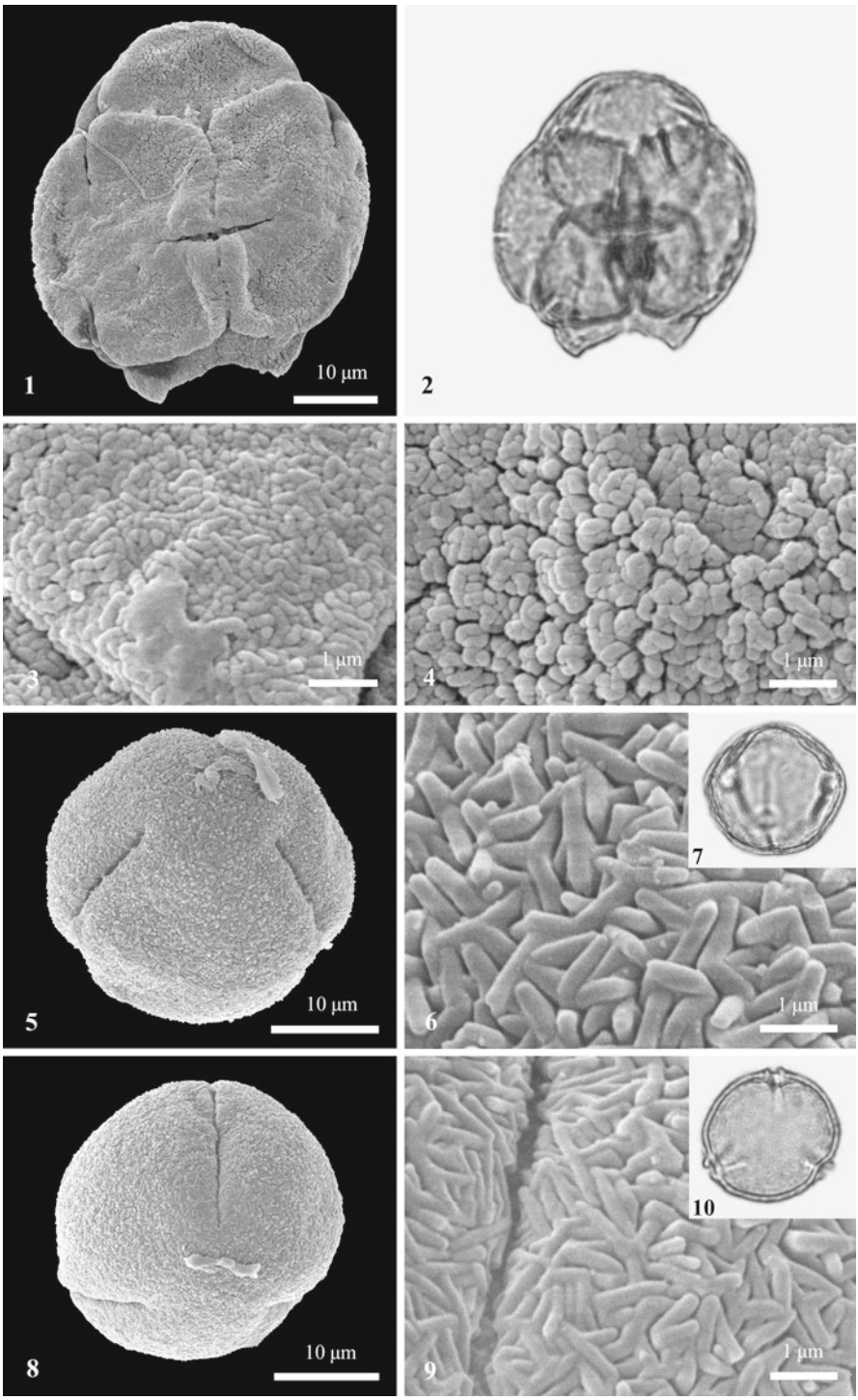



**Plate 7.12**

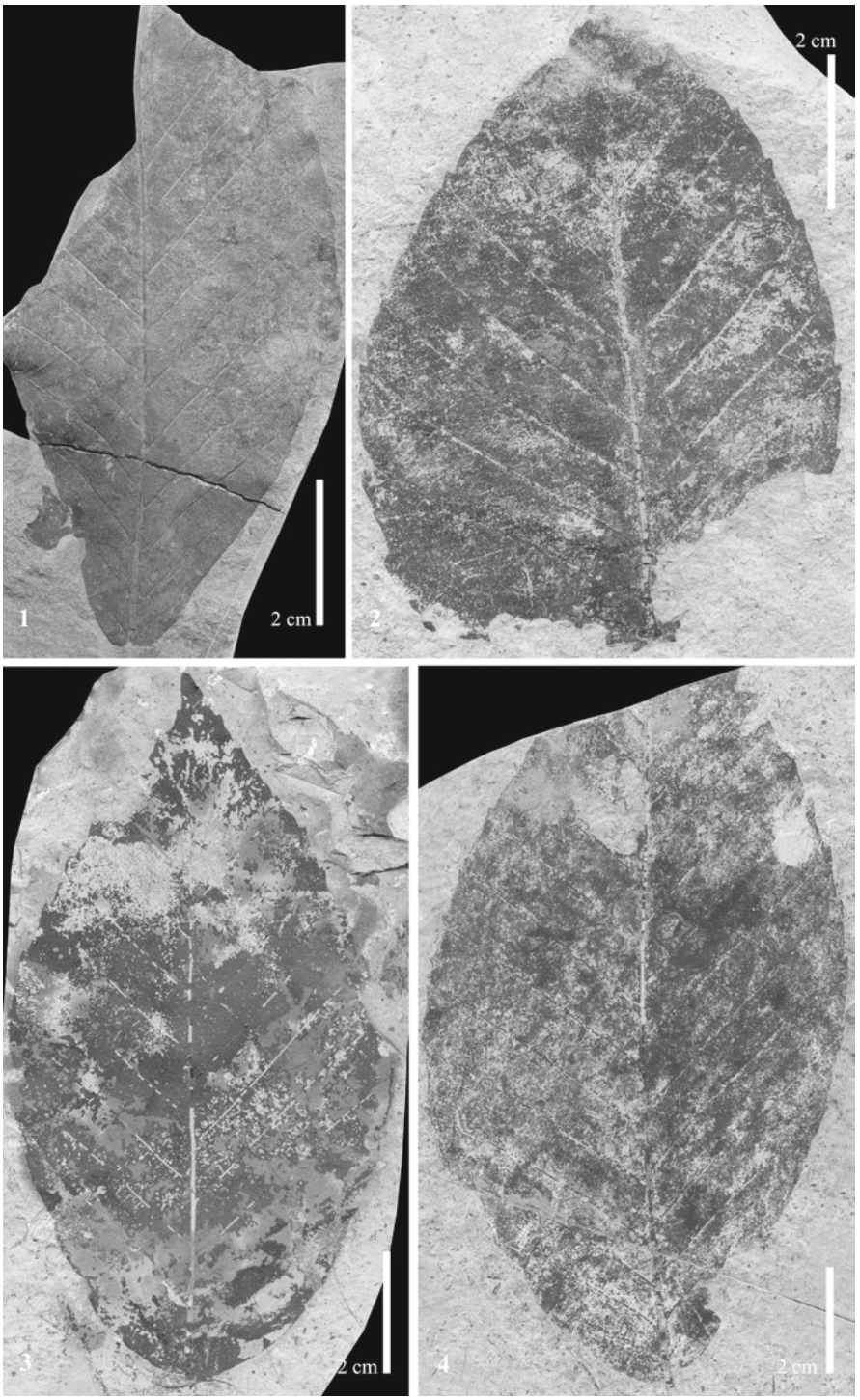



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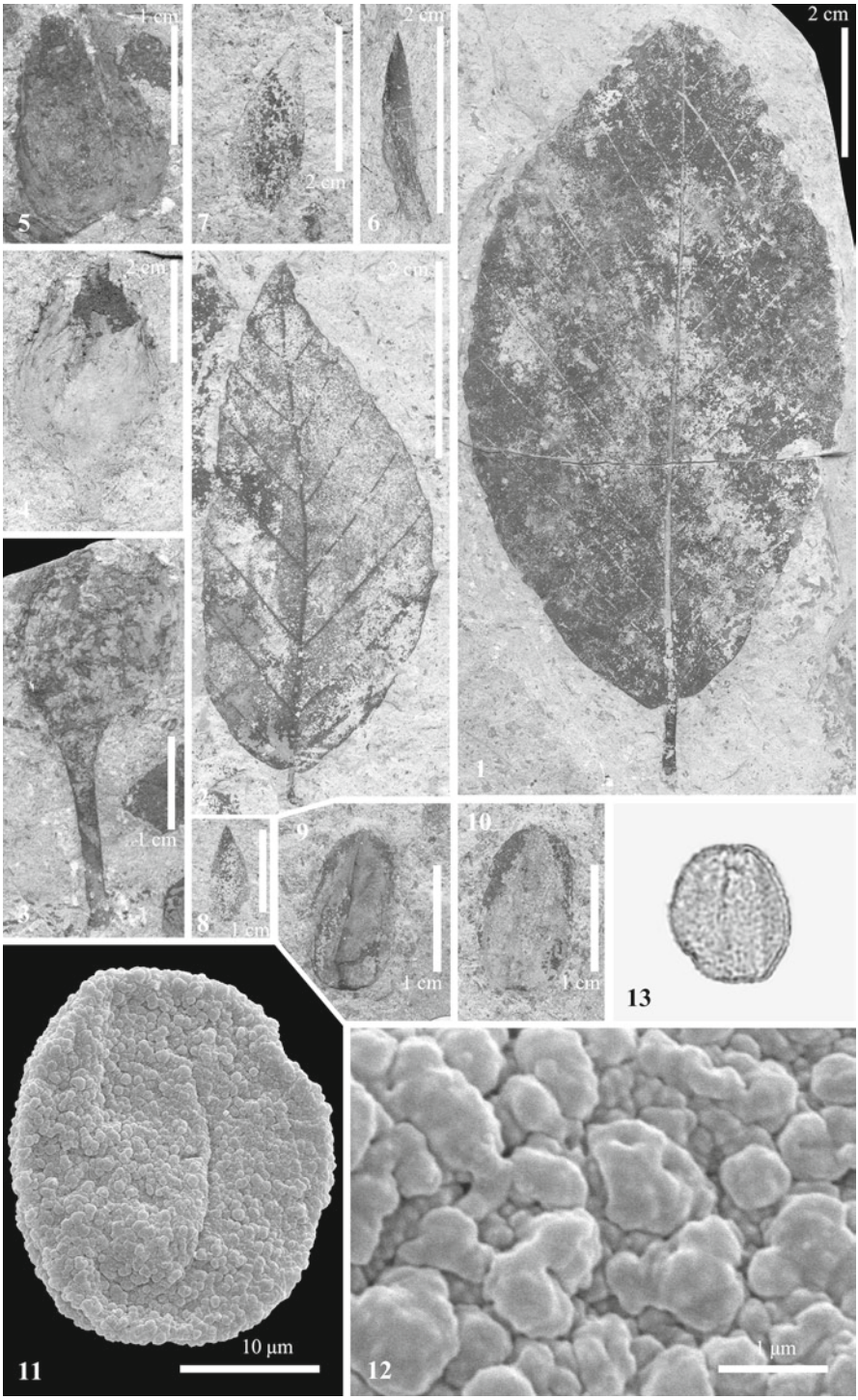

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**Plate 7.14**

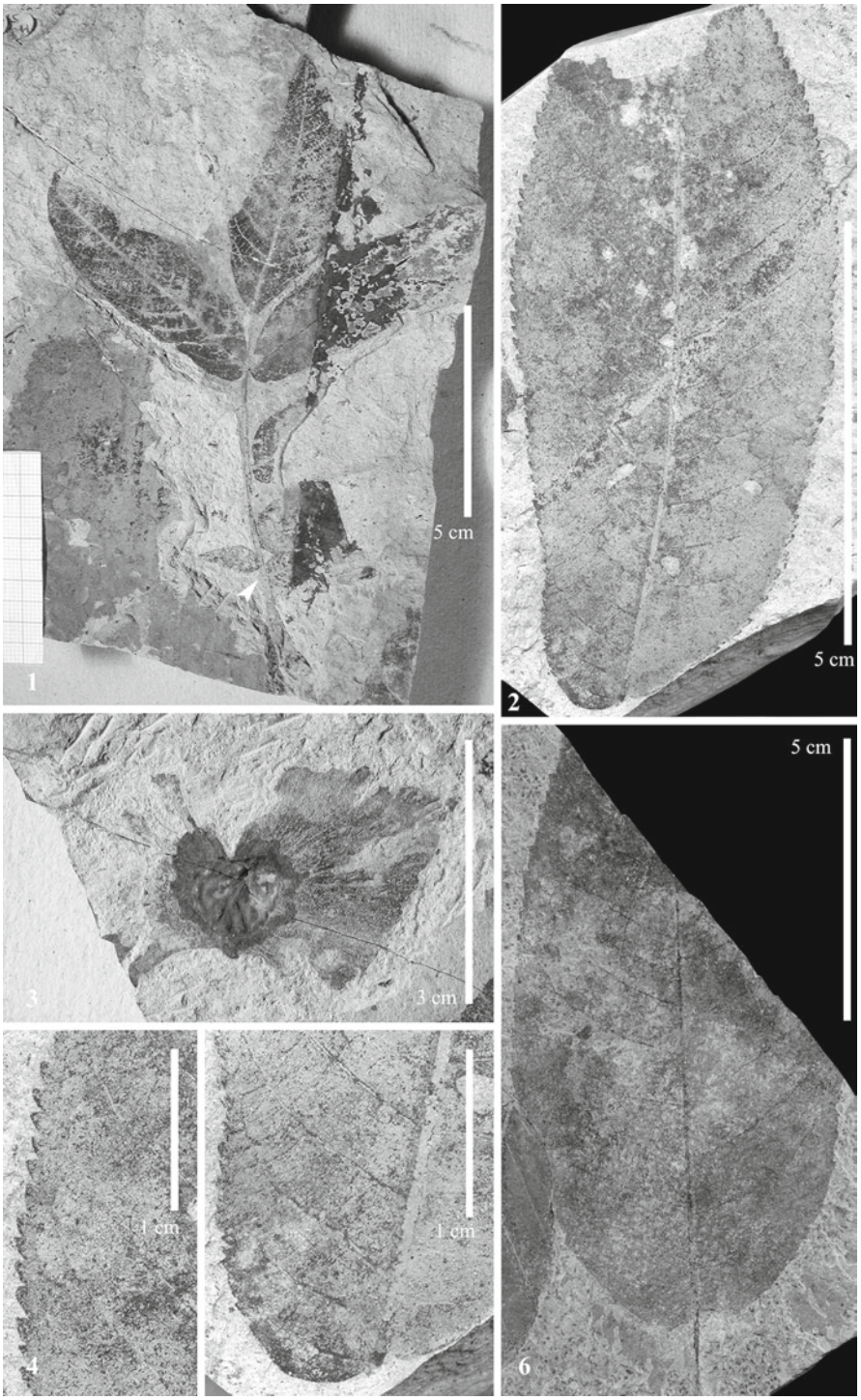



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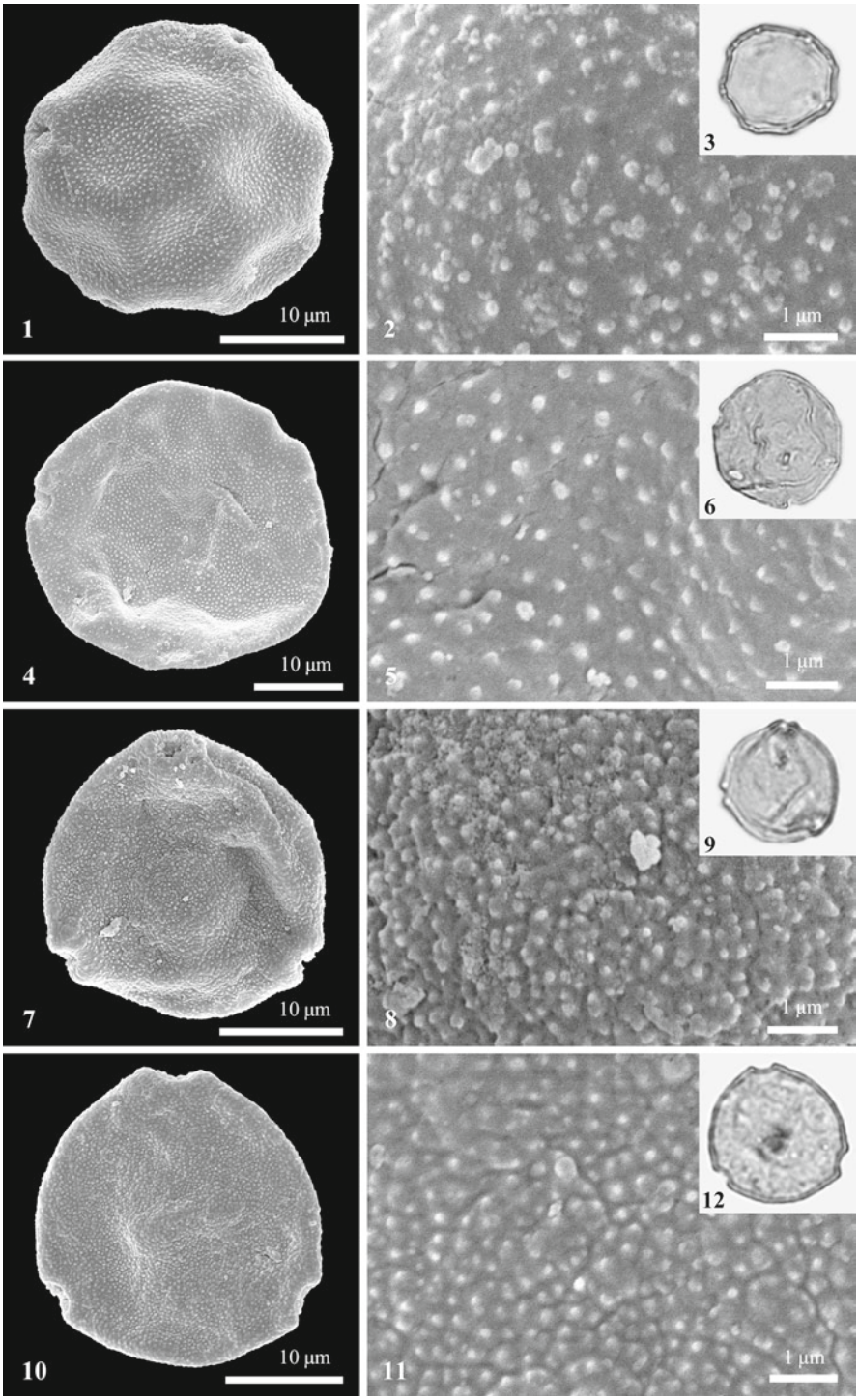



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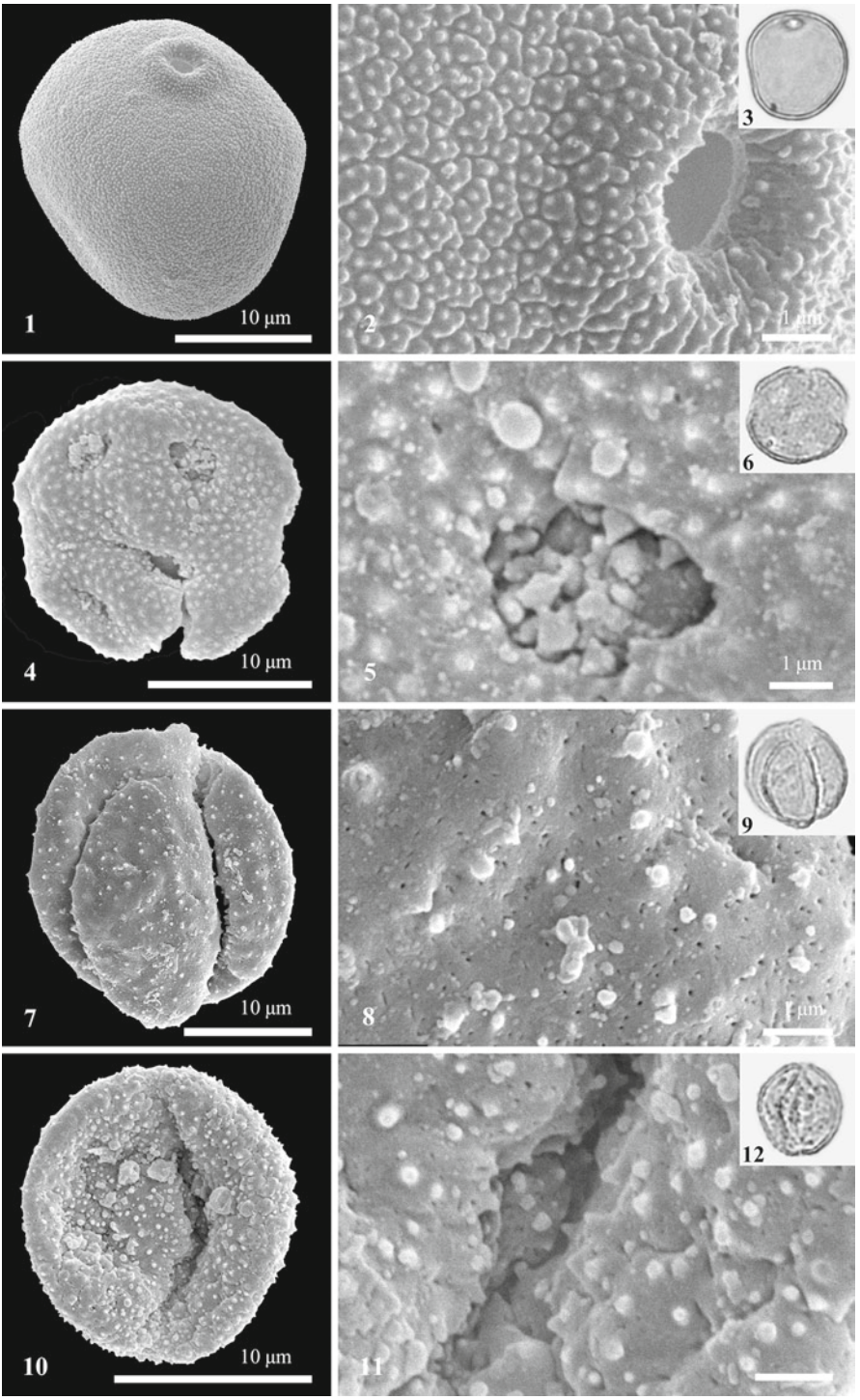



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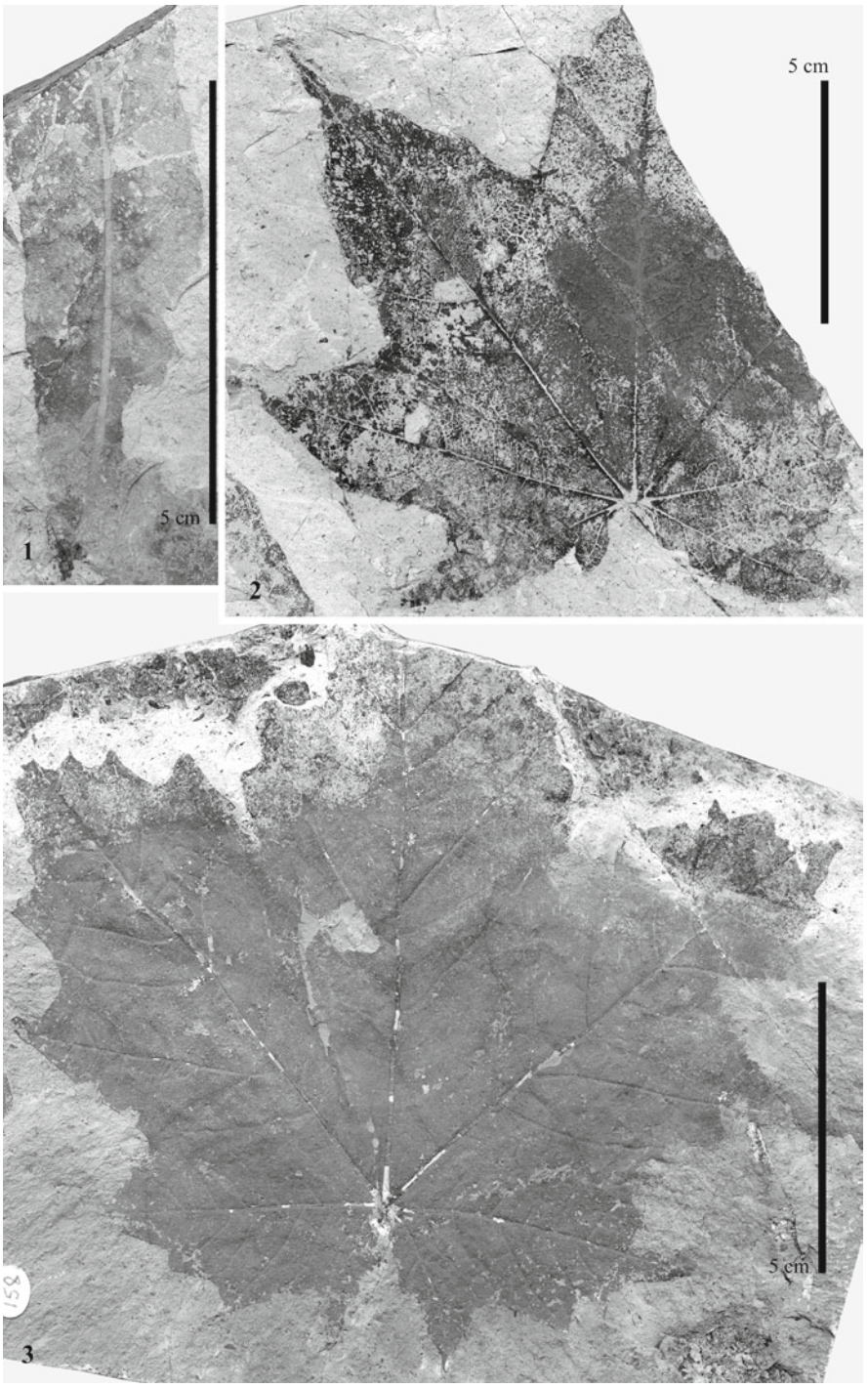



**Plate 7.18**

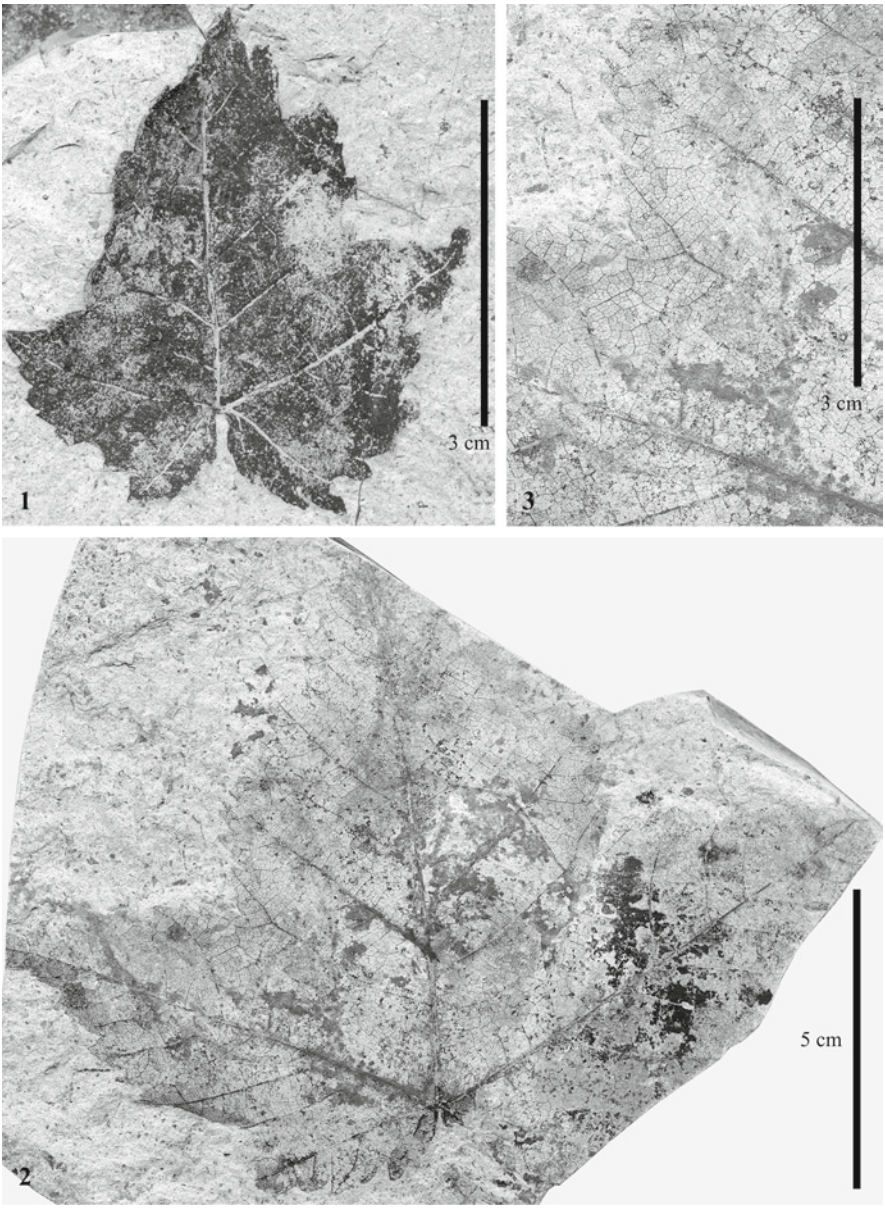



**Plate 7.19**

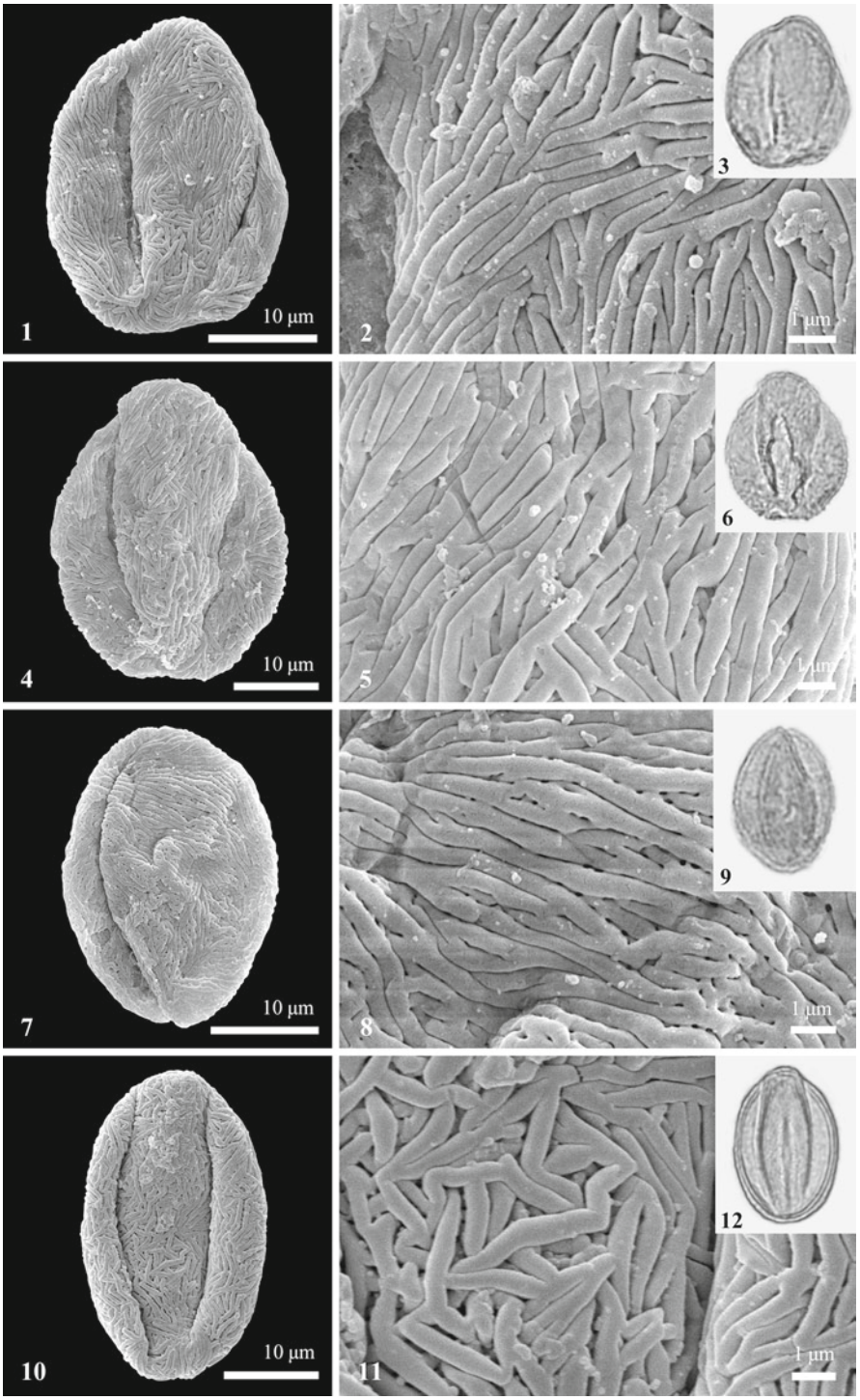



**Plate 7.20**

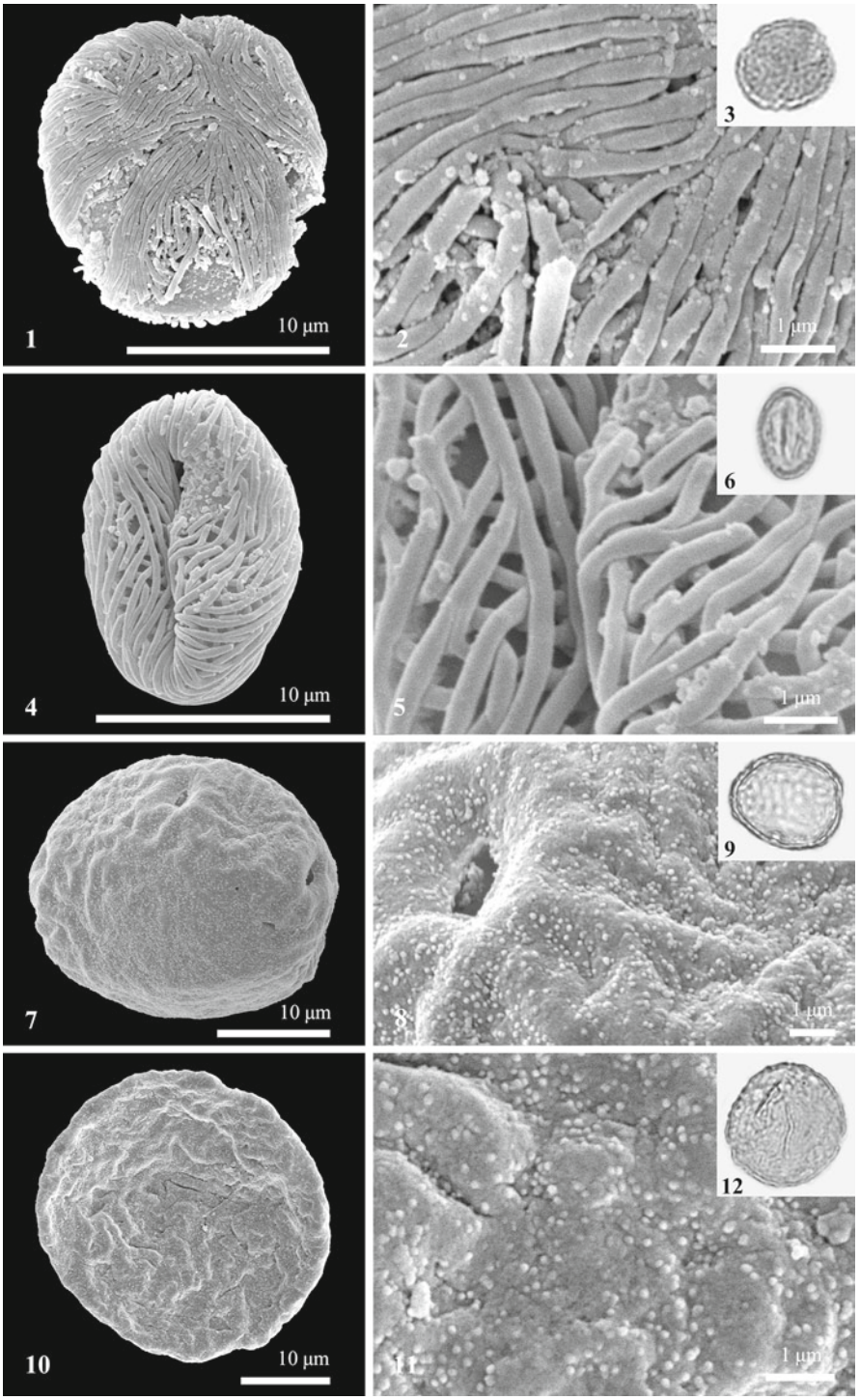



**Plate 7.21**

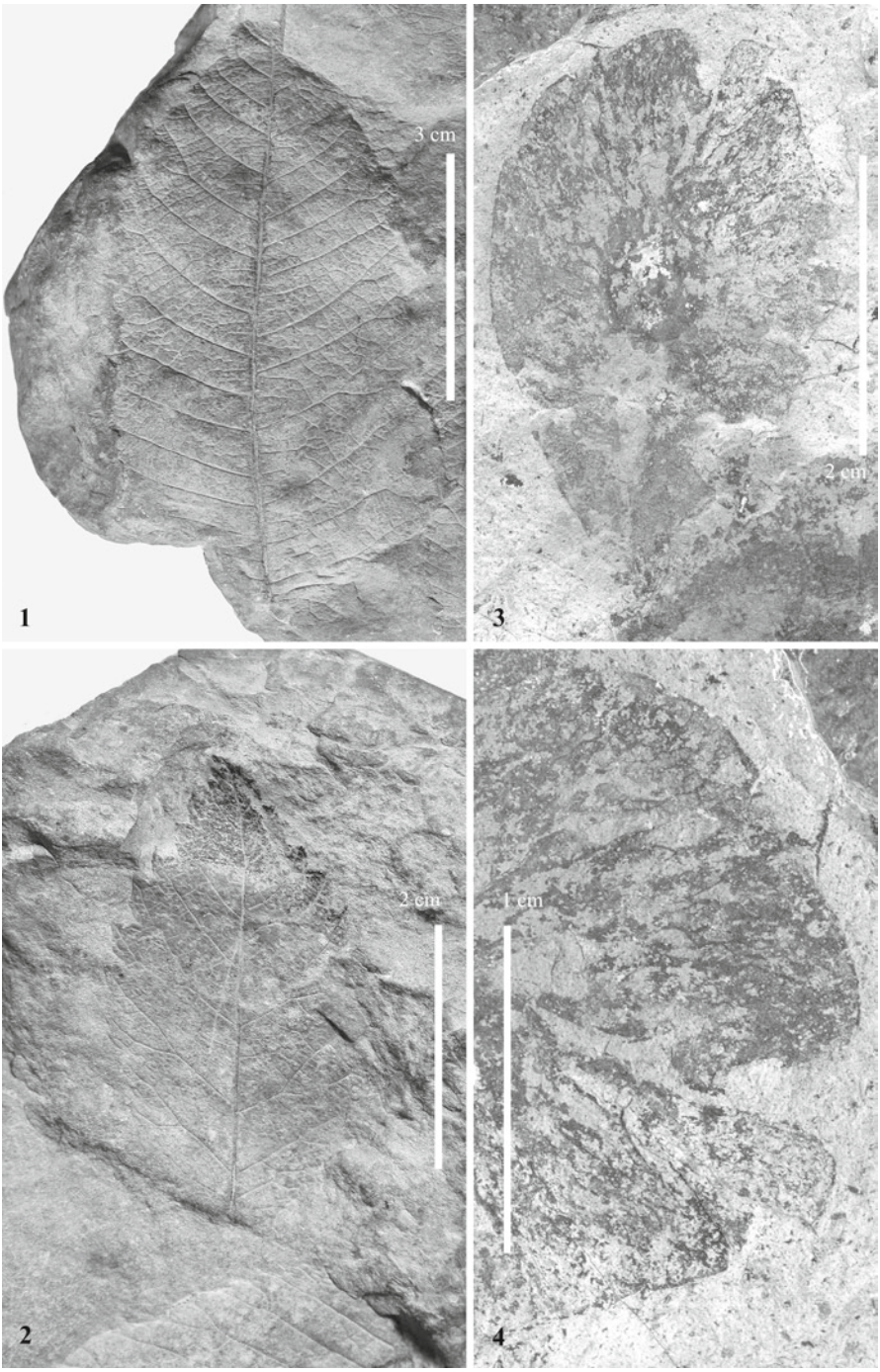



**Plate 7.22**

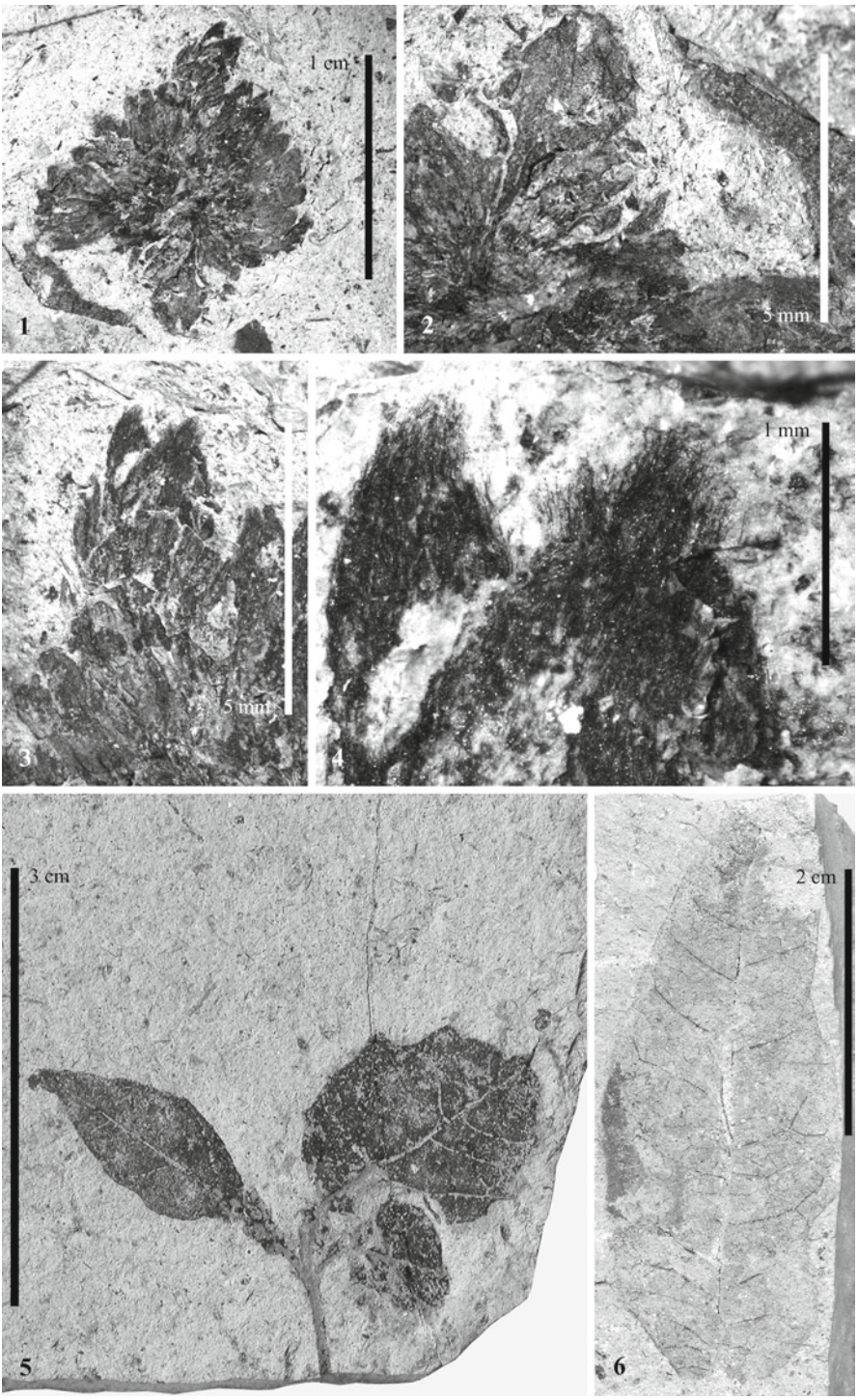



**Plate 7.23**

# Chapter 8
# A Lakeland Area in the Late Miocene

**Abstract** Fossil plants recovered from the Late Miocene (Messinian) Hreðavatn-Stafholt Formation grew in a landscape dominated by lakes of different sizes that were connected by small rivers and swampland. Well-drained areas bordering these wetlands were covered by mixed broadleaved deciduous and conifer forests dominated by Pinaceae, Rosaceae, and *Acer*. Relict taxa occurred both in wetlands (aff. Calycanthaceae) and hardwood forests (*Cyclocarya, Fagus, Tetracentron*). The flora and vegetation of the 7–6 Ma formation witnessed a cool temperate climate and the fairly high diversity of trees and shrubs was largely caused by relict taxa that persisted into the late Late Miocene and in some cases until the Early Pliocene. Although quite few taxa are new records for the Miocene flora of Iceland, one species of *Populus* resembling a poplar from the Middle Miocene of Siberia and from the Oligocene of Alaska may have first arrived to Iceland between 8 and 7 Ma. A general trend of impoverishment as seen in the Icelandic floras is also seen in floras of Arctic North America and mid-latitude Europe.

## 8.1 Introduction

The sedimentary rocks of the Hreðavatn-Stafholt Formation have been extensively studied, and their occurrence, variability, and age are well-established (Jóhannesson 1972, 1975, 1980; Franzson 1978; Ragnarsdóttir 1979; McDougall et al. 1977; Akhmetiev et al. 1978; Grímsson 2002, 2007). The plant fossils of the Hreðavatn Stafholt Formation were first studied by Heer (1859, 1868). In his first account on plant fossils from Iceland, Heer (1859) recognized, among others, *Pinus, Quercus, Betula, Alnus, Acer, Carex*, and *Platanus* from the "Hredavatn" and *Ulmus* and *Corylus* from the "Langavasdalr" localities. Later, Lindquist (1947; *Betula*), and Friedrich and Símonarson (1976, 1982) and Símonarson and Friedrich (1983; *Acer*) studied particular genera from this formation. More comprehensive work on the macrofloras was conducted by Akhmetiev et al. (1978; including pollen), Grímsson (1999, 2002), and Denk et al. (2005). Previous work suggests that the plant

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assemblages recovered from the Hreðavatn-Stafholt Formation represent temperate to cool-temperate mixed boreal forests.

In this chapter, we provide an updated and revised list of taxa present in the 7–6 Ma sedimentary rock formation in Iceland. Vegetation types are described and climatic requirements of potential modern analogues of the fossil taxa are assessed. In addition, rare or overlooked taxa that have not previously been mentioned for this formation are discussed. The Messinian floras of Iceland are then compared to coeval floras from Arctic North America and Europe.

## 8.2 Geological Setting and Taphonomy

The late Late Miocene floras from Iceland are preserved in sedimentary rocks of the Hreðavatn-Stafholt Formation, 7–6 Ma (Jóhannesson 1975; McDougall et al. 1977), in West Iceland (Fig. 8.1a). The rocks of this formation accumulated in association with rift relocation, and are therefore part of a highly complex geological construction associated with rift extinction, rift ignition, uplifting, plateau break-up, erosion, subsidence, and sedimentation (cf. Jóhannesson 1980; Grímsson 2007).

Most of the Miocene basalts on the Northwest Peninsula and West Iceland were formed in the Snæfellsnes Rift Zone (SRZ, now extinct; see syncline on Fig. 1.10, Chap. 1), 15–7 Ma ago. Around 7 Ma, volcanic activity gradually ceased in the SRZ and started farther to the east, forming the now-active Western Rift Zone (WRZ; Fig. 1.10). The rift zones were probably coactive for some time while the SRZ gradually became extinct and the WRZ became more active (Jóhannesson 1980). As loading from volcanism increased around the newly-evolved rift zone, the bedrock was affected by tectonic forces; it broke, was tilted, sank in some areas and rose in others (note the anticline in Fig. 1.10 between the extinct SRZ and the active WRZ). This was followed by the erosion of elevated areas and the accumulation of sediments. Thus, the Hreðavatn-Stafholt Formation lies on tilted and eroded Miocene bedrock. The lavas below the formation dip 11–25°SE, and are between 13 and 8 Ma, depending on the locality (Moorbath et al. 1968; Jóhannesson 1972, 1975, 1980; Aronson and Saemundsson 1975; Ragnarsdóttir 1979). The sedimentary rocks of this formation can be traced quite easily from Mount Hafnarfjall (Borgarnes locality), up the fjord Borgarfjörður, along the rivers Hvítá and Norðurá (Stafholt, Laxfoss, and Veiðilækur localities), and to Lake Hreðavatn (Brekkuá, Snóksdalur, Hestabrekkur, Giljatunga, Fífudalur, Þrimilsdalur, and Fanná localities; see Fig. 8.1b, c). In the lake region, they can be traced westwards to the Langavatnsdalur valley (Langavatnsdalur locality), lake Hítarvatn, and the mountains Fagraskógarfjall and Kolbeinsstaðafjall (Jóhannesson 1972, 1975, 1980; Akhmetiev et al. 1978; Franzson 1978; Ragnarsdóttir 1979; Grímsson 1999, 2002, 2007). Lavas overlying the sedimentary rock formation are youngest in the southern part of its extension, and are approximately 6 Ma on Mount Hafnarfjall (Franzson 1978). The lavas become progressively older to the north and west, and are 7–6.5 Ma

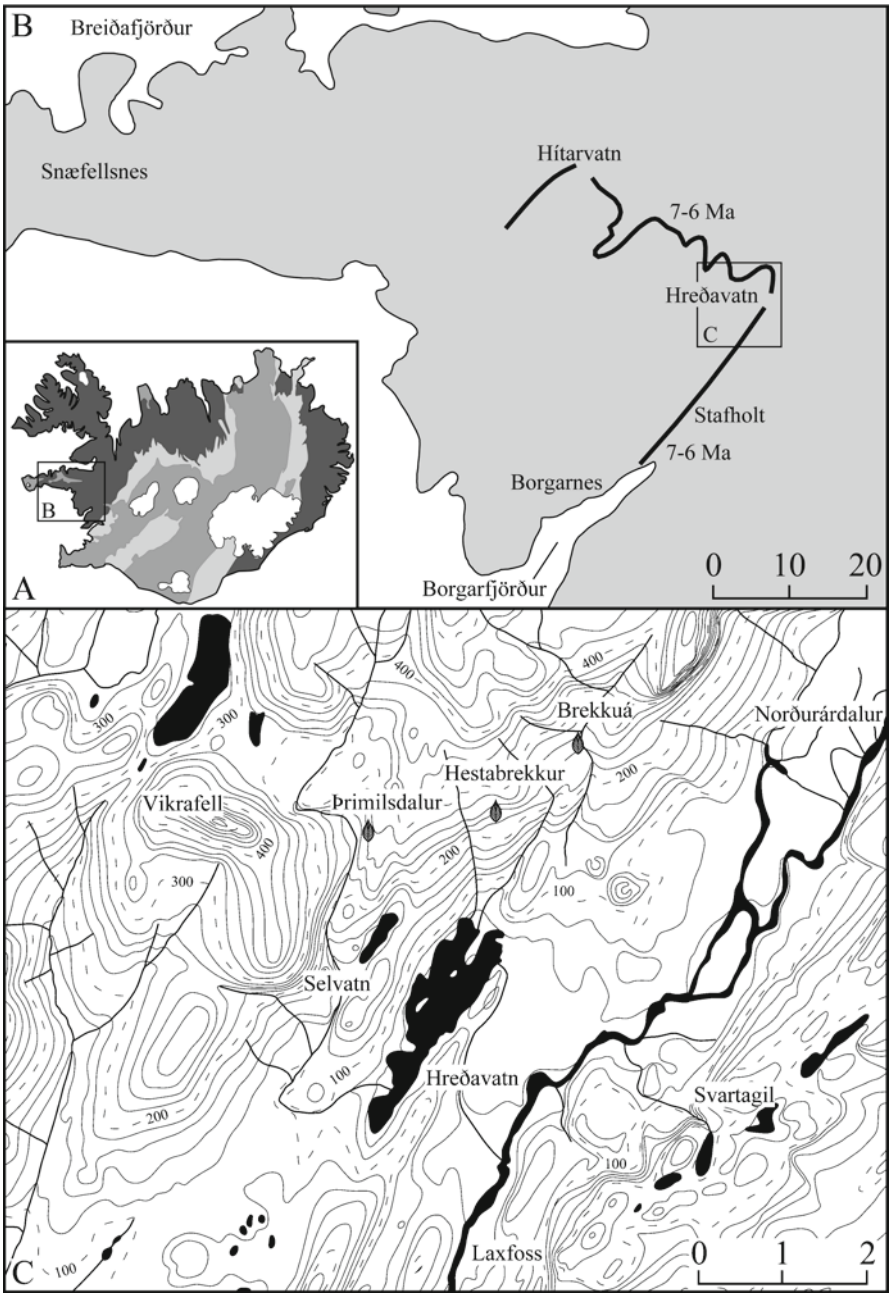



**Fig. 8.1** Map showing fossiliferous localities of the 7–6 Ma formation. (**a**) bedrock geology (see Fig. 1.10 for explanation), (**b**) extension of sedimentary rock formation, (**c**) Hreðvatn area (Geological background modified after Jóhannesson and Sæmundsson 1989; altitudinal lines from Landmælingar Íslands 1994)

at Lake Hreðavatn (Jóhannesson 1975; McDougall et al. 1977) where most of the fossiliferous outcrops are found.

The sedimentary rocks of this formation are extremely variable, mostly conglomerates, sandstones, and siltstones formed by erosion of elevated areas (Akhmetiev et al. 1978; Grímsson 2002, 2007). In areas of subsidence, several basins were formed with lakes and rivers. This resulted in fine-grained lake sediments, including organic-rich (plant detritus) siltstones, claystones, and diatomite, with associated coarse-grained fluvial sediments and lignites. Plant fossils are found in most of the clastic sedimentary rocks, but rarely in the volcanic units in the upper parts of the formation (Akhmetiev et al. 1978; Grímsson 2002, 2007).

The plant fossils found in the sedimentary rocks of the Hreðavatn-Stafholt Formation are preserved in different ways. Most occur as compressions revealed by fracture of the rock matrix exposing the often coalified plant remains. The preservation differs depending on the sedimentary rock type. Plant remains in the diatomite rich beds, and the ones composed mostly of fine-grained sedimentary rocks, are generally preserved as cleavage impressions or cleaved compressions (Chaloner 1999). In some localities where the sedimentary rocks are distinctly fractured, broken, and marked by water leakage, the fossils are preserved as true impressions only, with all organic material absent, and with only the faint markings of the plant visible. In beds composed of coarse-grained sedimentary rocks, plant fossils are also found as true impressions (Grímsson 2002).

## 8.3 Floras, Vegetation, and Palaeoenvironments

The floras of the 7–6 Ma formation include 30 taxa (Plates 8.1–8.16), the largest part of which (13 taxa) are woody angiosperms (Table 8.1, Fig. 8.2). Conifers (6 taxa), mosses and ferns (4 taxa), and herbaceous angiosperms (6 taxa) are equally represented. Overall, pollen and spores and, consequently, herbaceous taxa are underrepresented in this formation due to their generally bad preservation. Despite this, several taxa are characteristic of aquatic vegetation (*Ceratophyllum, Myriophyllum* and *Persicaria*). Lakes and ponds were probably interspersed in light swamp forests with *Alnus, Betula, Populus* and *Salix* (Fig. 8.3). Associated with rivers, temporally flooded backswamp forests perhaps also contained a plant with affinities to Calycanthaceae. Better drained areas were covered with broadleaved deciduous forests with few evergreen shrubs in the understorey, with conifers playing a more important role at higher elevations (Fig. 8.4). Although only few herbaceous taxa typical of meadows are preserved, this vegetation type was probably an important part of the landscape, forming a mosaic of forested and open areas. Meadows with an admixture of *Betula* were even more important at higher elevations with snow cover during the winter. Rocky outcrop forests not confined to a particular altitude were dominated by conifer species.

Overall, the palaeoenvironment at 7–6 Ma showed substantial similarities with modern southern boreal landscapes enjoying sufficient rainfall throughout the year

**Table 8.1** Taxa recorded for the 7–6 Ma floras of Iceland

| Hreðavatn-Stafholt Formation<br>Taxa | Pollen | Leaves | RP | Other | DM |
|---|---|---|---|---|---|
| Equisetaceae | | | | | |
| *Equisetum* sp. | | | | + | 1a |
| Lycopodiaceae | | | | | |
| *Huperzia* sp. | + | | | | la |
| Polypodiaceae | | | | | |
| Polypodiaceae gen. et spec. indet. 6 | + | | | | 1a |
| Incertae sedis – unassigned spores | | | | | |
| Trilete spore, fam., gen. et spec. indet. 1 | + | | | | 1a |
| Pinaceae | | | | | |
| *Abies steenstrupiana* | + | + | + D | + | 2a |
| *Larix* sp. | | + | | | 2a |
| *Picea* sect. *Picea* | + | + | + D | | 2a |
| *Pinus* sp. 1 | + | + | + | | 2a |
| *Pseudotsuga* sp. | | + | + | | 2a |
| *Tsuga* sp. | | + | + D | | 2a |
| Betulaceae | | | | | |
| *Alnus cecropiifolia* | + | + | + | | 1a, 2a |
| *Betula cristata* | (+) | + | (+) D | | 1a |
| Calycanthaceae | | | | | |
| aff. Calycanthaceae | + | | | | 1b |
| Caryophyllaceae | | | | | |
| Caryophyllaceae gen. et spec. indet. 3 | + | | | | 1b |
| Ceratophyllaceae | | | | | |
| *Ceratophyllum* sp. | | | + D | | 1b |
| Cyperaceae | | | | | |
| Cyperaceae gen. et spec. indet. B | | | + D | | 1b |
| Ericaceae | | | | | |
| *Rhododendron* aff. *ponticum* | | + | | | 1a?, 2a |
| Fagaceae | | | | | |
| *Fagus gussonii* | | + | + D | + | 2b, 3 |
| Juglandaceae | | | | | |
| *Cyclocarya* sp. | | + | | | 2a |
| Poaceae | | | | | |
| *Phragmites* sp. | | + | | + | 1b, 2a |
| Polygonaceae | | | | | |
| *Persicaria* sp. 1 | + | | | | 1b |
| Rosaceae | | | | | |
| cf. *Crataegus* sp. | | + | | | 1b |
| aff. *Sorbus* sp. (*S. aria* type) | | + | | | 1b |
| Rosaceae gen. et spec. indet. A | | + | | | 1b |
| Salicaceae | | | | | |
| *Populus* sp. B | | + | + | | 1a |
| *Salix gruberi* | | + | + | | |
| *Salix* sp. A | | + | | | 1a |

(continued)

**Table 8.1** (continued)

| Hreðavatn-Stafholt Formation<br>Taxa | Pollen | Leaves | RP | Other | DM |
|---|---|---|---|---|---|
| Sapindaceae | | | | | |
| *Acer askelssonii* | + | + | + D | | 2a |
| Scrophulariaceae | | | | | |
| aff. *Euphrasia* vel *Melampyrum* sp. | | + | | | 1b |
| Trochodendraceae | | | | | |
| *Tetracentron atlanticum* | + | + | + D | | 2a |
| Incertae sedis – Magnoliophyta | | | | | |
| Angiosperm fam. gen. et spec. indet. B | | + | | | ? |

*L* leafy axis, *A* fruit attached to leafy axis, *D* fruit dispersed, *RP* reproductive structure, + organ present, + original description of species based on this organ, (+) organ belonging to genus but uncertain to which of the species, (+) *2* indicating number of pollen types possibly belonging to the eponymous morphotaxon, *DM* Dispersal mode, *1a* wind long distance (anemochory), *1b* bird long distance (endozoochory), *2a* wind short distance (anemochory), *2b* animals short distance (exozoochory), *3* dyschory

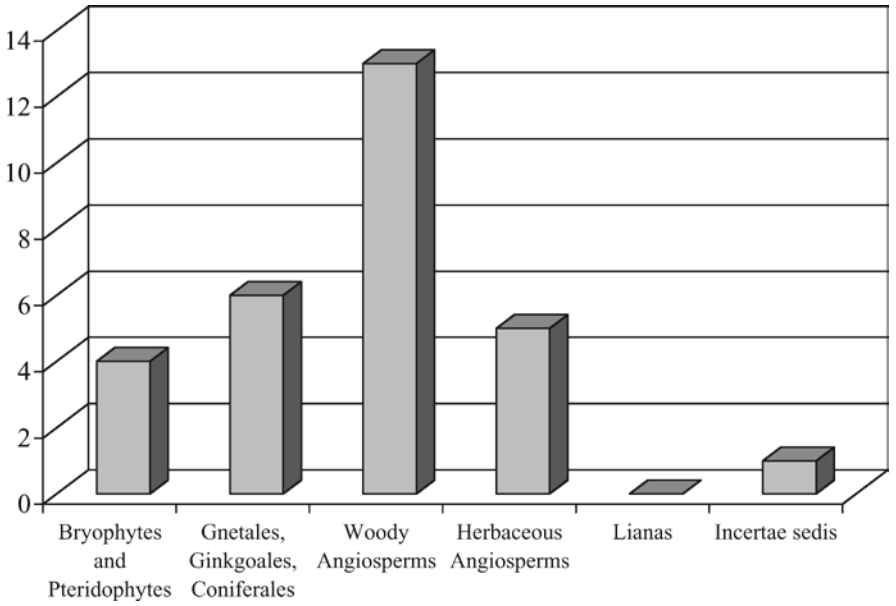



**Fig. 8.2** Distribution of life forms and higher taxa among the plants from the 7–6 Ma formation from Iceland. Height of columns indicates number of taxa

(see, for example, Jonsell 2004). Compared to modern landscapes, however, relicts from older formations persisted in the Hreðavatn-Stafholt Formation (*Fagus, Tetracentron, Rhododendron ponticum* type). These may have been confined to

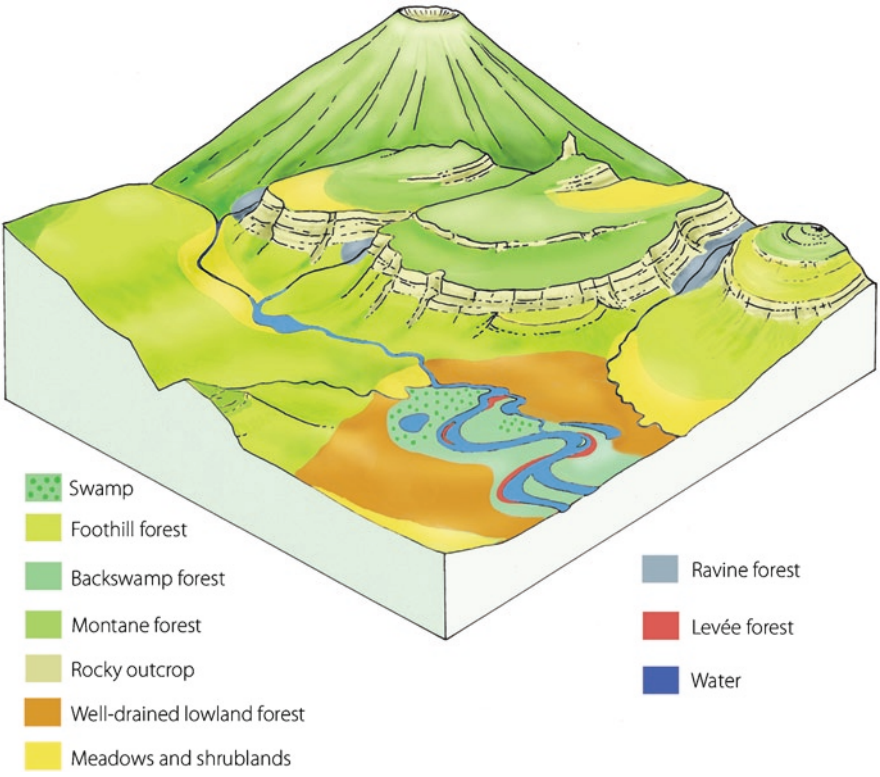



**Fig. 8.3** Schematic block diagram showing landscapes and vegetation types for the late Late Miocene (middle Messinian) of Iceland. Note extensive wetlands in the lowlands. See Table 8.2 for species composition of vegetation types

micro-climatically favourable sites. The general similarity with modern vegetation might reflect the fact that, from the Messinian onwards, an additional factor affecting climate and vegetation in Iceland has been the higher probability of local glaciers (Eiríksson 2008).

## 8.4 Ecological and Climatic Requirements of Modern Analogues

Most taxa recorded for the 7–6 Ma formation are indifferent to moderate variations in climate (Chap. 13, Appendix 13.1). A typical conifer in the 7–6 Ma formation is *Pseudotsuga*. At present, this genus comprises five species in western North America and East Asia. *Pseudotsuga macrocarpa* (Vasey) Mayr is endemic to southwestern California, where it occurs from 200 to 2,400 m a. s. l. in a

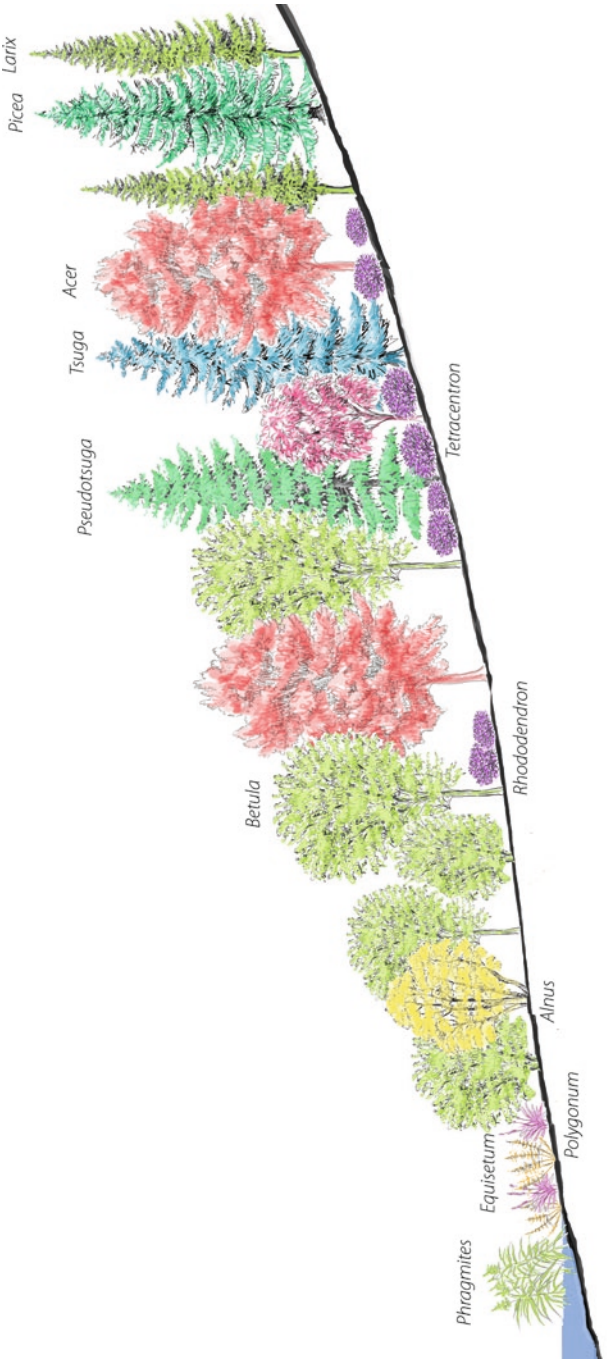



**Fig. 8.4** Schematic transect showing transition from lakeshore vegetation to a well-drained foothill forest

**Table 8.2** Vegetation types and their components during the late Late Miocene (middle Messinian) of Iceland. The palaeoecology of fossil species is reconstructed from their sedimentological context and ecology of modern analogues

**Vegetation types 7–6 Ma**

**AZONAL VEGETATION**

**Aquatic vegetation**
*Equisetum* sp.
*Ceratophyllum* sp.
*Myriophyllum* sp.
*Phragmites* sp.
*Persicaria* sp. 1
Cyperaceae gen et. spec. indet. 2

**Swamp vegetation**
*Equisetum* sp.
*Alnus cecropiifolia*
*Ceratophyllum* sp.
*Myriophyllum* sp.
*Persicaria* sp. 1
*Populus* sp. 2
*Salix* sp.
Cyperaceae gen et. spec. indet. 2

**Backswamp forests and temporally flooded lake margin**
Polypodiaceae gen. et spec. indet. 6
*Alnus cecropiifolia*
*Betula cristata*
aff. Calycanthaceae
*Phragmites* sp.
*Persicaria* sp. 1
*Populus* sp. 2
*Salix* sp.

**Levée forests and well drained lake margins**
Polypodiaceae ge. et spec. indet. 6
*Alnus cecropiifolia*
*Betula cristata*
aff. Calycanthaceae
cf. *Crataegus* sp.
*Salix* sp.
Rosaceae gen. et spec. indet. A
*Acer askelssonii*

**ZONAL VEGETATION**

**Well-drained lowland forests and lake margins**
*Alnus cecropiifolia*
*Betula cristata*
Rosaceae gen. et spec. indet. A
*Acer askelssonii*
*Fagus gussonii*
*Populus* sp. 2

**Foothill forests**
Polypodiaceae ge. et spec. indet. 6
*Alnus cecropiifolia*
*Betula cristata*
*Fagus gussonii*
*Cyclocarya* sp.
Rosaceae gen. et spec. indet. A
*Acer askelssonii*
*Tetracentron atlanticum*

**Montane forests**
*Abies steenstrupiana*
*Larix* sp.
*Picea* sp.
*Tsuga* sp.
*Pseudotsuga* sp.
*Fagus gussonii*
*Tetracentron atlanticum*

**Meadows and shrublands**
*Equisetum* sp.
*Huperzia* sp.
*Betula* sp. 1
Caryophyllaceae gen. et spec. indet. 3
*Persicaria* sp. 1
*Salix* sp.

**Ravine forests**
Polypodiaceae ge. et spec. indet. 6
*Abies steenstrupiana*
*Fagus gussonii*
*Acer askelssonii*

**Rocky outcrop forests**
*Larix* sp.
*Picea* sp.
*Pinus* sp. 1
*Tsuga* sp.
cf. *Crataegus* sp.
aff. *Sorbus* sp.

Mediterranean Csb climate (Kottek et al. 2006) with MAT 9–18°C. In contrast, *Pseudotsuga menziesii* (Mirb.) Franco has a much wider distribution in western North America and is a species with a very wide ecological range. Its vertical distribution is from 0 to 3,000 m a. s. l. with MAT ranging from −3.9°C to 24.8°C (Thompson et al. 1999). Also, the East Asian species typically grow at high elevations. *Pseudotsuga forrestii* Craib, endemic of Yunnan, is found between 2,400 and 3,300 m a. s. l. where it thrives under a Cwb climate according to Köppen (Kottek et al. 2006). *Pseudotsuga sinensis* Dode is a more common species in southern China and Taiwan, with a vertical range from 600 to 3,300 m a. s. l.; it thrives under winter dry or fully humid warm temperate climates (Cwa/b, Cfa/b). *Pseudotsuga brevifolia* W. C. Cheng & L. K. Fu is again a narrow endemic of southern China, currently restricted to an elevation of ca 1,300 m a. s. l. This species also grows in temperate Cwa and Cfa climates.

*Alnus cecropiifolia* is a large-leaved alder that is typical of Miocene floras across Europe. In Iceland, its stratigraphical range is from 12 to 3.8 Ma. Morphologically, this taxon is very similar to the western Eurasian *Alnus glutinosa* (L.) Gaertn, which has a wide distribution from southern Europe to western Siberia and northern Africa. It is a typical element of communities in places with stagnant water and riparian forests. It grows from sea level up to 1,800 m a. s. l. in Csb, Cfb, Dfa, Dfb and Dfc climates (Meusel et al. 1965; Kottek et al. 2006) with MAT –3.3°C to 17.4°C (MAT from Utescher and Mosbrugger 2009).

The fossil taxon *Betula cristata* is endemic to Iceland where it has a stratigraphic range from 9 to 5.5 Ma. This species resembles the East Asian *B. maximowicziana*, which is a prominent tree in the cool temperate zone of Japan, from eastern Honshu to Hokkaido (Ohwi 1965). *Betula maximowicziana* is a pioneer tree on open sites, and is a dominant element in climax forests from 1,000 to 1,900 m a. s. l. (Tsuda and Ide 2009), where it thrives under Cfb, Dfb and Dfc climates with MAT 3.1–13.5°C (MAT from Utescher and Mosbrugger 2009).

Fossil leaves very similar to *Populus* sp. B from the 7–6 Ma formation have been compared to the modern *P. trichocarpa* Torrey & A. Gray and to the Chinese species *P. szechuanica* C. K. Schneid. by Irina A. Iljinskaja (in Budantsev 2005). *Populus trichocarpa* is a species with a wide ecological breadth and a distribution in western North America including Alaska. It grows from sea level to 3,000 m a. s. l. in floodplains, at lake margins or on subalpine slopes (Flora of North America Editorial Committee 2010) with MAT –6.7°C to 17.2°C (Thompson et al. 2000). *Populus szechuanica* occurs in Tibet, Gansu, Shaanxi, Sichuan and Yunnan between 1,100 and 4,600 m a. s. l. (Flora of China Editorial Committee 1999).

*Tetracentron* is a monotypic genus with only one living species, *Tetracentron sinense* Oliv. This species is today restricted to central and southwestern China, northern Vietnam, northern Burma, and south of the Himalayas to northeastern India, Bhutan, and eastern Nepal. It forms part of broadleaved evergreen and mixed evergreen-deciduous forests and occurs at forest edges and along streams. The vertical distribution of *T. sinense* ranges from 1,100 to 3,500 m a. s. l. (Flora of China Editorial Committee 2001). It thrives in Cfa, Cwa and Cwb climates with MAT 2.2–19°C.

Generally, a cool temperate (mainly Cfb) climate is suggested based on the climatic requirements of all taxa recovered from the 7–6 Ma formation (for a complete list of potential modern analogues see Chap. 13, Appendix 13.1). *Fagus* is the most cold-sensitive taxon in the plant assemblage of this formation. Given the extremely rare occurrence of this taxon (as compared to the older 9–8 Ma formation) the climate experienced by the vegetation may have been close to the limit for *Fagus*. This would indicate a cool Cfb climate with MAT 6–8°C for the Hreðavatn-Stafholt Formation. The modern climate of Gothenburg may well illustrate this situation (see Fig. 7.6, 3, Chap. 7).

## 8.5 Taxonomic Affinities and Origin of Newcomers

Only a few taxa in the 7–6 Ma sedimentary rock formation are new records. Among the herbaceous plants, *Persicaria* aff. *amphibian* (L.) Gray and *Myriophyllum* are water plants that have a worldwide distribution at present. Their presence in the 7–6 Ma sediments may simply reflect the presence of more extensive wetlands as compared to the older formations (see also Sect. 8.6 for a similar trend in western Arctic North America).

Among macrofossils, the distinctive foliage of *Populus* sp. B is restricted to the 7–6 Ma formation. These leaves are similar to the Middle Miocene *P. aldanensis* Iljinsk. from central Yakutia, Siberia (Budantsev 2005), and have been compared by Irina A. Iljinskaja (in Budantsev 2005) to the Oligocene *P. congerminalis* A. Hollick (Hollick 1936) from the Alaskan Peninsula. Hollick (1936) also pointed out similarities of such leaves with the European *P. gaudinii* Heer, which Heer (1856) had described from the Miocene in Switzerland. Based on Heer's illustrations, it cannot be determined whether these specimens are closely similar to the Icelandic ones. Overall, the biogeographic pattern seen here, combining the fossil record in western North America and/or Central to East Asia with that from Iceland, is a recurrent theme for several plant taxa encountered from the Miocene in Iceland. Examples from older formations are *Fagus friedrichii* (Grímsson and Denk 2005; Denk and Grimm 2009), *Tetracentron* (Grímsson et al. 2008), and *Pseudotsuga* (Denk et al. 2005). How these taxa reached Iceland is difficult to determine. Poplars are wind-dispersed over long distances and *Populus* sp. B from the 7–6 Ma Hreðavatn-Stafholt Formation may have colonized Iceland either from the east or from the west.

## 8.6 Comparison to Coeval Northern Hemispheric Floras

In western Arctic North America, the temperature was decreasing through the Late Miocene, reflected by the rising abundance of Ericales. White et al. (1997) analysed 23 samples from the Canyon Village locality dated by $^{40}Ar/^{39}Ar$ to $6.57 \pm 0.02$ Ma.

The palynological record is dominated by Betulaceae, Pinaceae, Ericales, Salicaceae, and *Sphagnum*. Canopy openness and regional paludification increased, expressed by the high number of *Sphagnum* spores. Cooler conditions as compared to older floras in this area are interpreted as reflecting the Messinian event.

In Western Europe, rich plant assemblages from Late Miocene localities in Central France dated by K-Ar as 10–6 Ma (Gilbert et al. 1977) reflect a pronounced cooling between the early Late Miocene and the latest Late Miocene. The Cheylade and Capels localities (Laurent and Marty 1927; Appendix 8.1) are dated as 7–6 Ma. Laurent and Marty's (1927) determinations are not reliable in all cases (for example, their herbaceous taxa based on leaf imprints), but many of the woody angiosperm genera reported by them appear to be correctly identified (*Carpinus, Fagus*, *Juglans*, *Platanus, Sassafras*, *Ulmus*). The two floras are (warm) temperate in appearance and resemble both extant and Pontian (Messinian) floras of Georgia, Transcaucasia (Kolakovski 1964; Denk et al. 2001).

The rich flora of Vegora is another example of a Messinian (ca 6 Ma; Kvaček et al. 2002) flora at mid-latitudes (northern Greece). Due to its more southern position, this flora does not show evidence of distinct cooling (Appendix 8.1). A substantial number of taxa at the generic level are also found in the Messinian and older floras of Iceland, but genera such as *Acer, Alnus* and *Quercus* are much more diverse in Vegora than in the Miocene of Iceland. At the same time, warmth-loving elements such as *Chamaerops, Daphnogene* or *Zelkova* have never been reported from Iceland. Overall, the Vegora flora represents a fully humid warm temperate (warm Cfa variant) climate not comparable to the conditions in Iceland at that time.

The more distinct difference between high latitude and mid-latitude floras during the Messinian most likely reflects the first radiation of northern hemispheric glaciations at around 7 Ma, involving glaciers on mountaintops in Iceland (Thiede et al. 1998; Eiríksson 2008).

## 8.7 Summary

The fossil plant assemblages from the 7–6 Ma (Messinian) sedimentary rock formation in Iceland reflect the flora and vegetation that grew in and around extensive wetlands with interspersed small lakes and ponds, rivers and swamp forests. While the dominating species are typical elements of the (southern) boreal zone (*Betula cristata*), a number of relict taxa persisted from earlier periods. The most warmth-demanding element, *Fagus*, had become a very rare element in the Messinian floras of Iceland. However, well-drained hardwood forests contained evergreen shrubs in the understorey. The spread of boreal vegetation in Iceland may have been related to the intensification of glaciation at about 7.1 Ma as seen in Greenland, the Iceland and the Vöring plateaus.

Among the newly immigrating elements were water plants and a species of *Populus*. These taxa are not indicative of a particular migration route to Iceland; they are long distance-dispersed by birds or wind and hence are uninformative as to whether an active "North Atlantic land bridge" existed during the Messinian.

# Appendix 8.1

Floristic composition of the 7–6 Ma sedimentary formation of Iceland compared to contemporaneous northern hemispheric fossil assemblages at mid and high latitudes.

| **Hreðavatn-Stafholt flora, Iceland [64°46´N, 21°34´E] 7-6 Ma** This study | |
|---|---|
| 2 | Equisetum sp. |
| 1 | Huperzia sp. |
| 1 | Polypodiaceae gen.et spec. indet. 6 |
| 1 | Trilete spore, fam., gen. et spec. indet. 1 |
| 1-3 | Abies steenstrupiana |
| 2,3 | Larix sp. |
| 1-3 | Picea sect. Picea |
| 1-3 | Pinus sp. 1 |
| 2,3 | Pseudotsuga sp. |
| 2,3 | Tsuga sp. |
| 1-3 | Acer askelssonii |
| 1-3 | Alnus cecropiifolia |
| 3 | Angiosperm fam. gen. et spec. indet. B |
| 1-3 | Betual cristata |
| 1 | aff. Calycanthaceae |
| 1 | Caryophyllaceae gen. et spec. indet. 3 |
| 2 | Ceratophyllum sp. |
| 3 | cf. Crataegus sp. |
| 1,3 | cf. Cyclocarya sp. |
| 2 | Cyperaceae gen. et spec. indet. B |
| 3 | Fagus gussonii |
| 3 | aff. Euphrasia vel Melampyrum sp. |
| 1 | Persicaria sp. 1 |
| 3 | Phragmites sp. |
| 3 | Populus sp. B |
| 1,3 | Rhododendron aff. ponticum |
| 3 | Rosaceae gen. et spec. indet. A |
| 2,3 | Salix gruberi |
| 2,3 | Salix sp. A |
| 3 | aff. Sorbus sp. (S. aria type) |
| 1-3 | Tetracentron atlanticum |

| **Capels and Cheylade, Central France [44°56´N, 2°40´E; 45°12´ N, 2°42´ E] 7-6 Ma** Laurent & Marty, 1927; Gibert et al., 1977 | |
|---|---|
| 3 | Goniopteris pulchella |
| 3 | Pteris aquilina |
| 3 | **Abies cf. pectinata** |
| 3 | **Acer cf. campestre** |
| 3 | **Acer pseudoplatanus** |
| 3 | **Alnus glutinosa** |
| 3 | Bambusa vel Arundinaria sp. |
| 3 | Berchemia volubilis |
| 3 | Castanea sativa |
| 3 | Cornus sanguinea |
| 3 | **Crataegus oxyacantha** |
| 3 | Diospyros cf. virginiana |
| 3 | **Fagus sylvatica var. pliocenica** |
| 3 | Fraxinus arvernensis |
| 3 | Helianthemum vulgare |
| 3 | Ilex aquifolium |
| 3 | Juglans regia |
| 3 | Juncus sp. |
| 3 | Menispermum europaeum |
| 3 | Platanus aceroides |
| 3 | **Populus balsamoides** |
| 3 | **Populus tremula** |
| 3 | Ranunculus cf. acris |
| 3 | Ranunculus cf. auricomus |
| 3 | Robinia arvernensis |
| 3 | Rubus niacensis |
| 3 | **Salix alba** |
| 3 | Sassafras ferrettianum |
| 3 | Scirpus sp. |
| 3 | Stachys laurenti |
| 3 | Ulmus effusa |
| 3 | Viburnum tinus |
| 3 | Viola cf. odorata |

| **Vegora flora, northern Greece [40°40´N, 21°42´E] 6 Ma** Kvaček et al., 2002 | |
|---|---|
| 3 | Osmunda parschlugiana |
| 3 | Ginkgo adiantoides |
| 2 | Cedrus vivariensis |
| 3 | Cupressus rhenana |
| 2,3 | Glyptostrobus europaeus |
| 2 | Keteleeria hoehnei |
| 3 | Pinaceae gen. indet. |
| 2 | **Pinus hampeana** |
| 2 | **Pinus salinarum** |
| 2 | **Pinus sp.** |
| 3 | **Pinus sp. 1** |
| 3 | **Pinus sp. 2** |
| 2 | **Pinus vegorae** |
| 3 | Sequoia abietina |
| 3 | Taxodium dubium |
| 3 | **Acer aegopodifolium** |
| 3 | **Acer integrilobum** |
| 2 | **Acer limburgense** |
| 3 | **Acer pseudomonspessulanum** |
| 3 | **Acer pyrenaicum** |
| 3 | **Acer sp.** |
| 2 | **Acer spp.** |
| 3 | **Acer subcampestre** |
| 3 | **Acer tricuspidatum** |
| 3 | **Alnus adscendens** |
| 3 | **Alnus cecropiifolia** |
| 2 | **Alnus cf. kefersteinii** |
| 3 | **Alnus ducalis** |
| 3 | **Alnus gaudinii** |
| 3 | **Alnus julianiformis** |
| 3 | **Betula pseudolumnifera** |
| 2 | Carpinus betulus foss. |
| 3 | Carpinus grandis |
| 2 | Carpinus kisseri |
| 2 | Castanea sp. |
| 3 | Chamaerops humilis foss. |
| 2 | Craigia bronnii |
| 3 | Daphnogene pannonica |
| 3 | Dicotylophyllum sp. 1 – sp. 6 |
| 2 | **Fagus decurrens** |
| 3 | **Fagus gussonii** |
| 2 | Fraxinus sp. |
| 3 | Hedera multinervis |
| 3 | Laurophyllum pseudoprinceps |
| 3 | Laurophyllum sp. |
| 3 | Leguminosites sp. |
| 3 | Monokotyledonae gen. indet. |
| 3 | Platanus leucophylla |
| 2 | Platanus sp. |
| 3 | **Populus balsamoides** |
| 3 | **Populus populina** |
| 3 | **Populus sp. 1** |
| 3 | **Populus sp. 2** |
| 3 | Pterocarya paradisiaca |
| 2 | Quercus cerrisaecarpa |
| 3 | Quercus drymeja |
| 3 | Quercus gigas |
| 3 | Quercus kubinyii |
| 3 | Quercus mediterranea |
| 3 | Quercus pseudocastanea |
| 3 | Quercus sosnowskyi |
| 2 | Quercus sp. |
| 3 | Quercus sp. |
| 3 | Sassafras ferrettianum |
| 3 | Ulmus plurinervia |
| 2,3 | Zelkova zelkovifolia |

Boldface indicates that genus is present in the Hreðavatn-Stafholt Formation. Grey shading indicates that the genus is present in younger (5.5 Ma) and older formations. *1* based on pollen, spores; *2* based on leaves and/or fruit/seed fossils; *3* based on leaf fossils

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# Explanation of Plates

**Plate 8.1** **1**. Lake Hreðavatn, western Iceland, Hreðavatn-Stafholt Formation (ca 7–6 Ma), showing the Hreðavatn farm in the middle right of photo. **2**. Overview towards the east, showing part of the Hreðavatn lake and the dip of surrounding lavas. Mountains in the background are positioned on the far side of the river Norðurá. **3**. The Brekkuá outcrop, river delta and shallow lake sediments. **4**. Hestabrekkur outcrop, fine grained shallow to deep-water lake sediments, contains the best preserved fossils of this formation. **5**. Close-up of diatomite rich siltstone units at the Brekkuá outcrop, dark spots on yellow flakes are plant remains. **6**. Volcanic breccia overlying the clastic units at Brekkuá. **7**. Siltstones, sandstones and fine tephra layers at the Hestabrekkur outcrop. **8**. Massive glassy tephra from the upper sedimentary unit of the Brekkuá outcrop. **9–12**. Fossils are preserved as compressions or impressions mostly in siltstones (**9**) or diatomite (**10–12**) but are also found in the different volcanic tephra units in the upper part of the sequence

**Plate 8.2** **1**. *Equisetum* sp. (IMMH). **2–4**. Polypodiaceae gen. et spec. indet. 6. **2**. Spore in SEM, equatorial view. **3**. Detail of spore surface. **4**. Spore in LM, equatorial view. **5–7**. Polypodiaceae gen. et spec. indet. 1. **5**. Spore in SEM, equatorial view. **6**. Detail of spore surface. **7**. Spore in LM, equatorial view. **8–10**. *Huperzia* sp. **8**. Spore in SEM, proximal polar view. **9**. Detail of spore surface. **10**. Spore in LM, proximal polar view

**Plate 8.3** **1–11**. *Abies steenstrupiana*. **1**. Leaf, flat needle with twisted base (IMNH). **2**. Leaf, needle (IMNH). **3**. Leaf, medium sized needle (IMNH). **4**. Leaf, medium sized needle (IMNH). **5**. Cone scale, small (GM 6722). **6**. Cone scale, medium sized (GM 6742). **7**. Cone scale, large sized (IMNH). **8**. Cone scale, large sized (IMNH). **9**. Winged seed (GM 6736). **10**. Branch with leaf scars (IMNH 2026-02). **11**. Branch with leaf scars (IMNH 2026-01)

**Plate 8.4** **1–4**. *Pinus* sp. 1 (Diploxylon type). **1**. Bisaccate pollen grain in SEM, polar view. **2**. Detail of pollen grain surface. **3**. Bisaccate pollen grain in LM, polar view. **4**. *Pinus* sp., long narrow needles (IMNH). **5**. *Pinus* sp., winged seed (GM 6731). **6**. *Pinus* sp., winged seed (IMNH 3163). **7**. *Pinus* sp., winged seed (IMNH 1983). **8**. *Pseudotsuga* sp., large female cone (IMNH). **9**. *Pseudotsuga* sp., counterpart to Fig. 8. **10**. *Tsuga* sp., leaf, short flat needle (GM 6740). **11**. *Tsuga* sp., leaf (GM 6738). **12**. *Tsuga* sp., leaf (S 094080). **13**. *Tsuga* sp., small winged seed (IMNH)

**Plate 8.5** **1**. *Alnus cecropiifolia*, medium sized elliptic leaf (IMNH). **2**. *Alnus cecropiifolia*, small wide elliptic leaf (IMNH). **3**. *Alnus kefersteinii*, female infructescences (IMNH). **4**. *Alnus kefersteinii*, large female infructescences (S 106900-3). **5**. *Alnus kefersteinii*, female infructescence (IMNH). **6**. *Alnus kefersteinii*, female infructescence (IMNH 1974-01)

**Plate 8.6** **1–9**. *Betula cristata*. **1**. Medium sized wide elliptic leaf with cordate base (IMNH). **2**. Medium sized elliptic leaf (S 094978). **3**. Detail of Fig. 2 showing teeth along margin. **4**. Small narrow elliptic leaf with cordate base (IMNH org 177). **5**. Upper part of a leaf (IMNH). **6**. Detail showing venation and teeth along basal margin (IMNH). **7**. Small elliptic leaf with semi-acute base (IMNH 4670). **8**. Medium sized ovate leaf (IMNH). **9**. Small narrow elliptic leaf with a long petiole (IMNH 5186)

**Plate 8.7** **1–11**. *Betula cristata*. **1**. Small fruit scale with short round lateral lobes (IMNH). **2**. Fruit scale (S094927-1). **3**. Small fruit scale with wide parallel sided central lobe (GM 6759). **4**. Medium sized fruit scale with narrow lateral lobes (IMNH). **5**. Fruit scale with tong-like lobes (IMNH). **6**. Fruit scale with a long and narrow central lobe and round lateral lobes (IMNH).

**7**. Large fruit scale (IMMH). **8**. Large fruit scale (GM 6769). **9**. Winged seed, nutlet wide elliptic (IMNH). **10**. Winged see, nutlet round (IMNH). **11**. Winged seed, styles long (IMNH). **12–15**. *Ceratophyllum* sp. **12**. Endocarp with several spines (IMNH 5184). **13**. Part of endocarp (IMNH 1984). **14**. Endocarp with spines (IMNH). **15**. Endocarp with prominent spines (IMNH)

**Plate 8.8** **1–3**. *Alnus* sp. 1. **1**. Pollen grain in SEM, polar view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, polar view. **4–6**. *Betula* sp. **4**. Pollen grain in SEM, polar view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, polar view. **7–9**. aff. Calycanthaceae **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view. **10–12**. Caryophyllaceae gen. et spec. indet. 3. **10**. Pollen grain in SEM. **11**. Detail of pollen grain surface. **12**. Pollen grain LM

**Plate 8.9** **1–5**. Cyperaceae gen. et spec. indet. B. **1**. Achene, elliptic with style base (IMNH). **2**. Achene, wide elliptic (IMNH). **3**. Achene, round (IMNH). **4**. Achene, wide elliptic (IMNH). **5**. Achene, narrow elliptic (IMNH). **6–8**. *Rhododendron* aff. *ponticum*. **6**. Large elliptic leaf (IMNH 3160A). **7**. Detail of Fig. 6 showing basal part of leaf and marginal venation. **8**. Medium sized elliptic leaf (IMNH org 178)

**Plate 8.10** **1**. *Fagus gussonii*, upper half of a small leaf (IMNH). **2**. Large nut with parts of wings extending along the upper part (IMNH). **3**. *Phragmites* sp., part of rhizome (IMNH 1986). **4**. *Phragmites* sp., part of stem/leaf (S 094976)

**Plate 8.11** **1–3**. *Persicaria* sp. 1. **1**. Pollen grain in SEM. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM. **4–6**. *Salix* sp. 2. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7–9**. *Acer* sp.1. **7**. Pollen grain in LM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view. **10–12**. *Acer* sp. 1. **10**. Pollen grain in SEM, equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM. **13–15**. *Tetracentron atlanticum*. **13**. Pollen grain in SEM, equatorial view. **14**. Detail of pollen grain surface. **15**. Pollen grain in LM, equatorial view

**Plate 8.12** **1**. aff. *Sorbus* sp. (*S. aria* type), wide elliptic leaf with acute base (IMNH). **2**. Detail of Fig. 1 showing teeth and marginal venation. **3**. aff. *Sorbus* sp. (*S aria* type), small leaf with long petiole (IMNH). **4**. Rosaceae gen. et spec. indet. A, lower part of large leaf (IMNH). **5**. Detail of Fig. 4 showing teeth and marginal venation (IMNH). **Plate 8.12** (continued) **6**. cf. *Crataegus* sp., fragment of leaf (S 094081-01). **7**. Detail of Fig. 6 showing teeth

**Plate 8.13** **1**. *Populus* sp. B, upper half of lamina (IMNH). **2**. *Populus* sp. C, female catkin with fruits (IMNH). **3**. *Populus* sp. C, part of female catkin with fruits (IMNH). **4**. *Salix gruberi*, part of lamina (S 094107). **5**. Detail of Fig. 4 showing marginal venation. **6**. *Salix gruberi*, detail showing marginal venation. **7**. *Salix* sp., capsule with two recurved valves (S 094075). **8**. *Salix* sp. A, medium sized narrow elliptic leaf (IMNH). **9**. *Salix* sp. A, small elliptic leaf (IMNH). **10**. Salix sp. A, large narrow elliptic leaf (IMNH)

**Plate 8.14** **1**. *Acer askelssonii*, very large leaf (IMNH). **2**. *Acer askelssonii*, small leaf (IMNH)

**Plate 8.15** **1**. *Acer askelssonii*, small leaf (IMNH). **2**. *Acer askelssonii*, medium sized leaf (S 106579). **3**. *Acer askelssonii*, samara (S 116469). **4**. *Acer askelssonii*, samara, counterpart to Fig. 3. (IMNH org 44). **5**. *Acer askelssonii*, samara (IMNH org 43)

**Plate 8.16** **1**. aff. *Euphrasia* vel *Melampyrum* sp., small leaf (IMNH). **2**. *Tetracentron atlanticum*, large ovate leaf (IMNH). **3**. Detail of Fig. 2 showing teeth along margin. **4**. Angiosperm fam. gen. et spec. indet. B, numerous slender axes with awl-shaped leaves (IMNH 5187)

# Plates




**Plate 8.1**

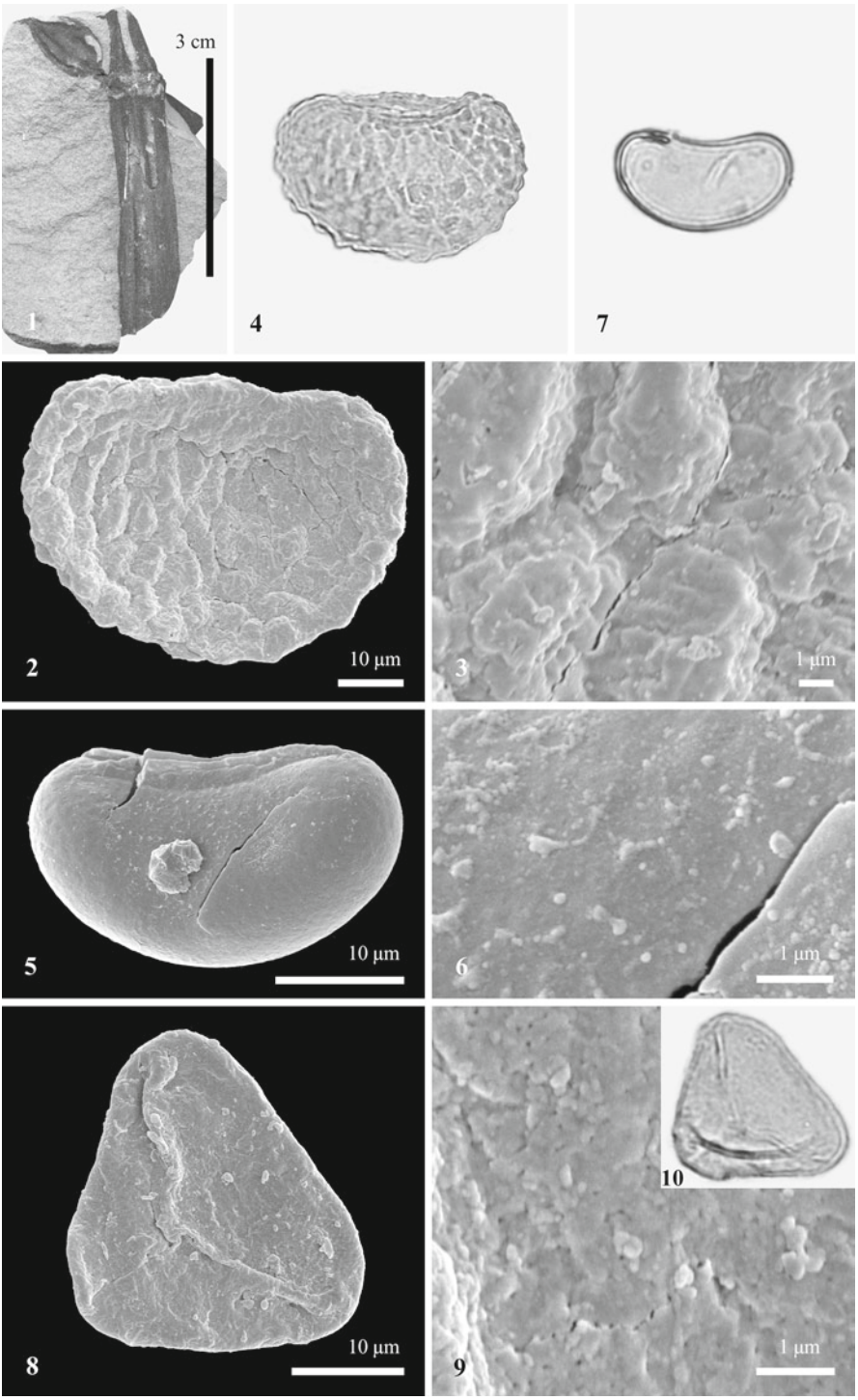



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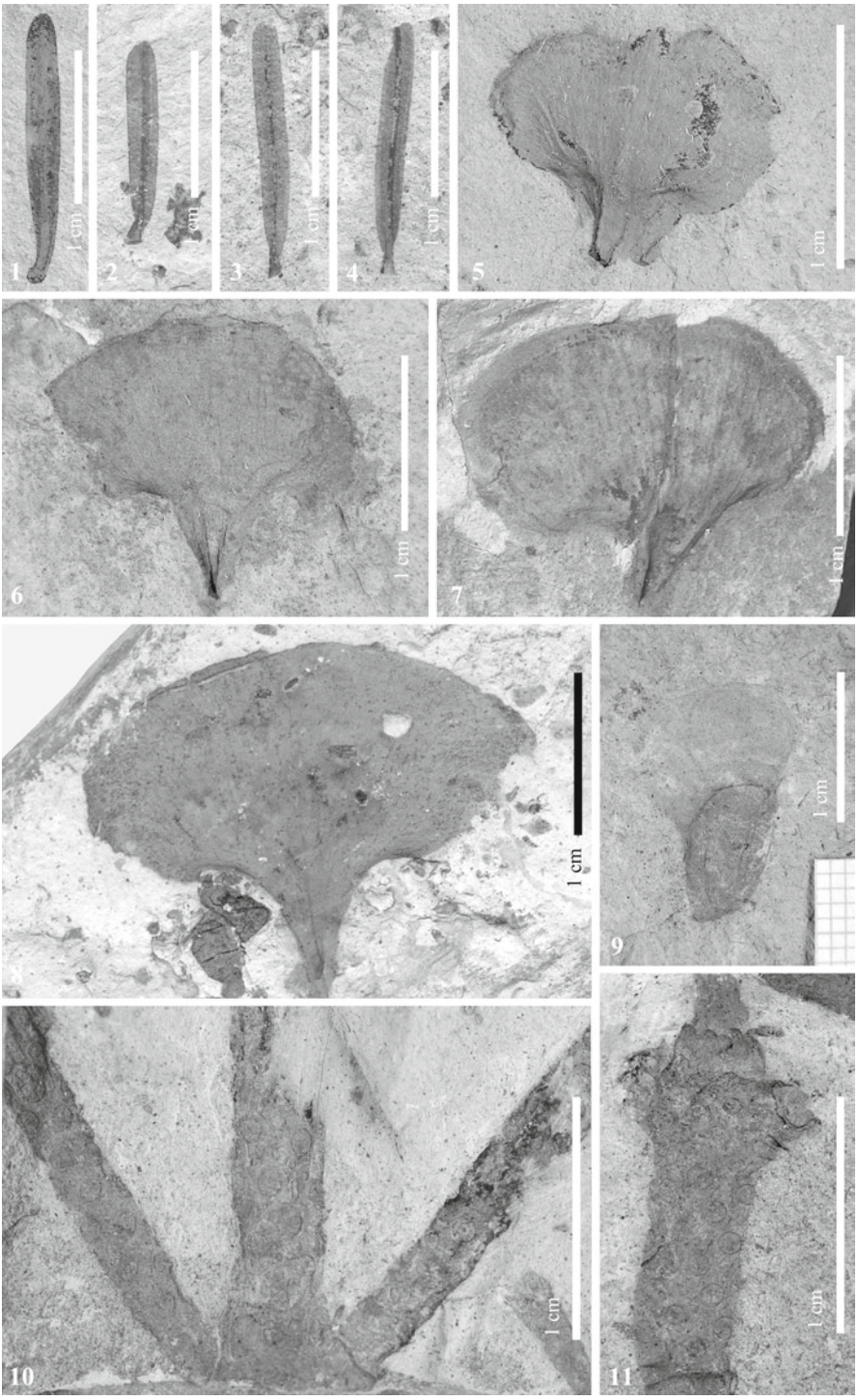



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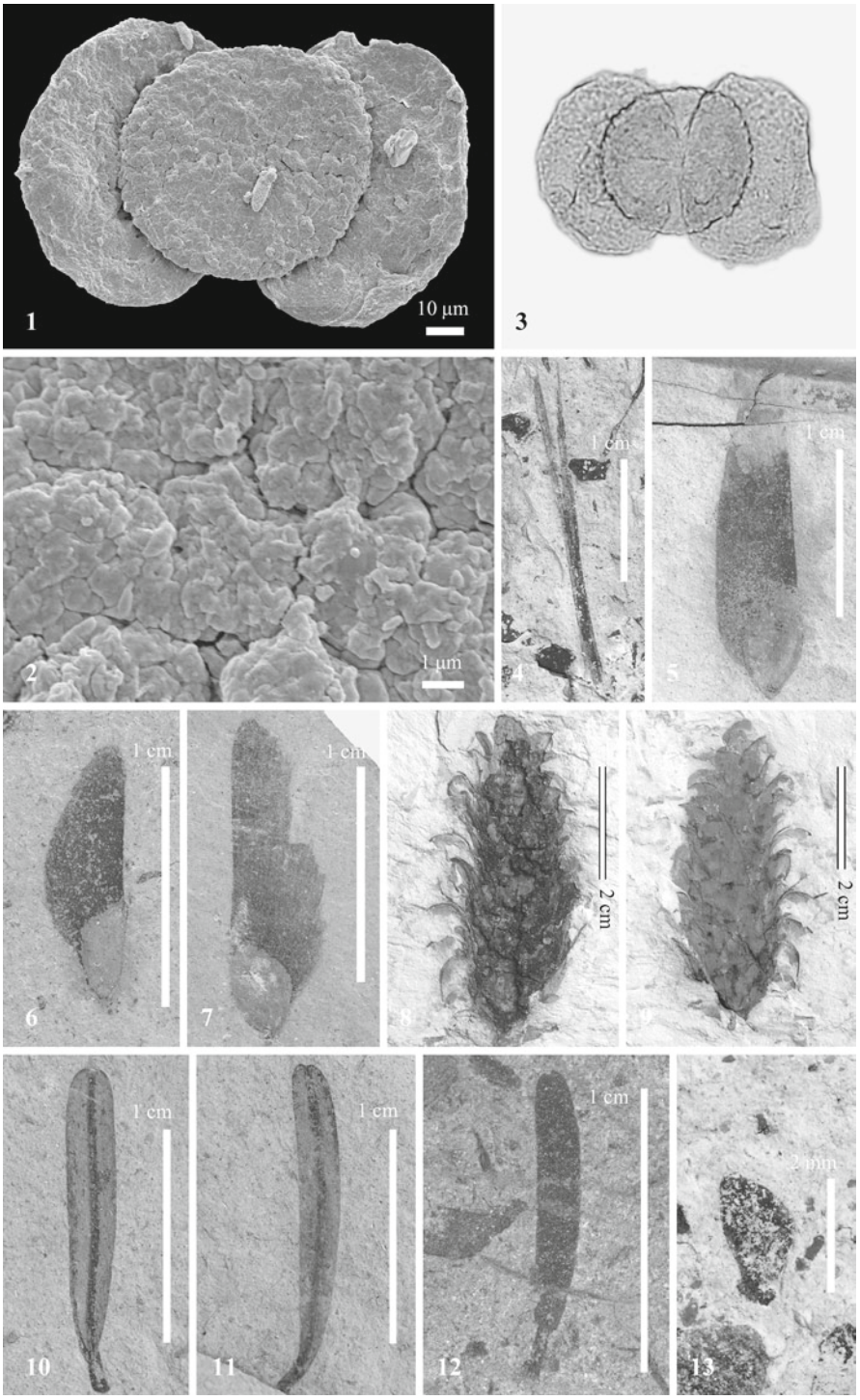

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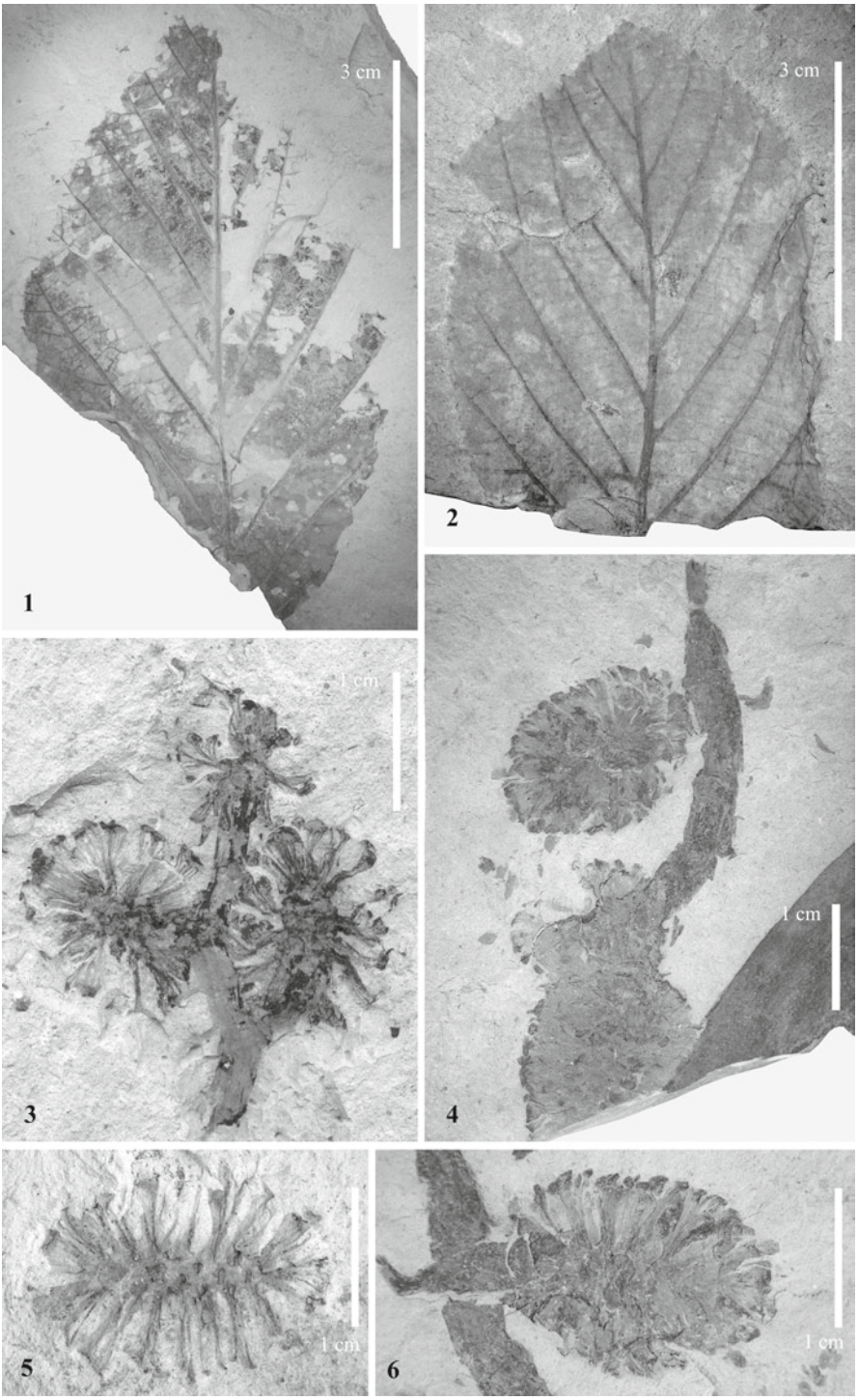



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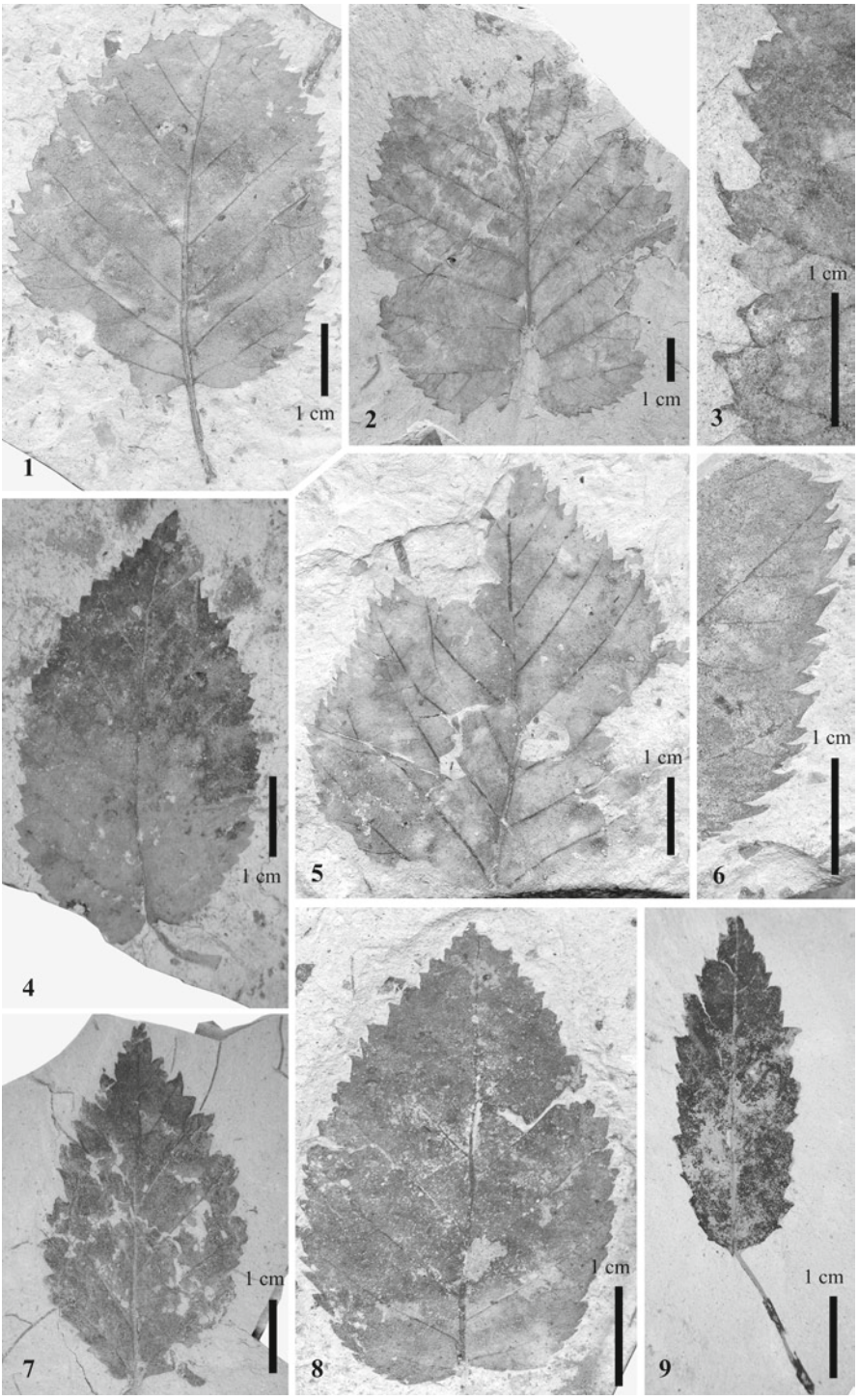



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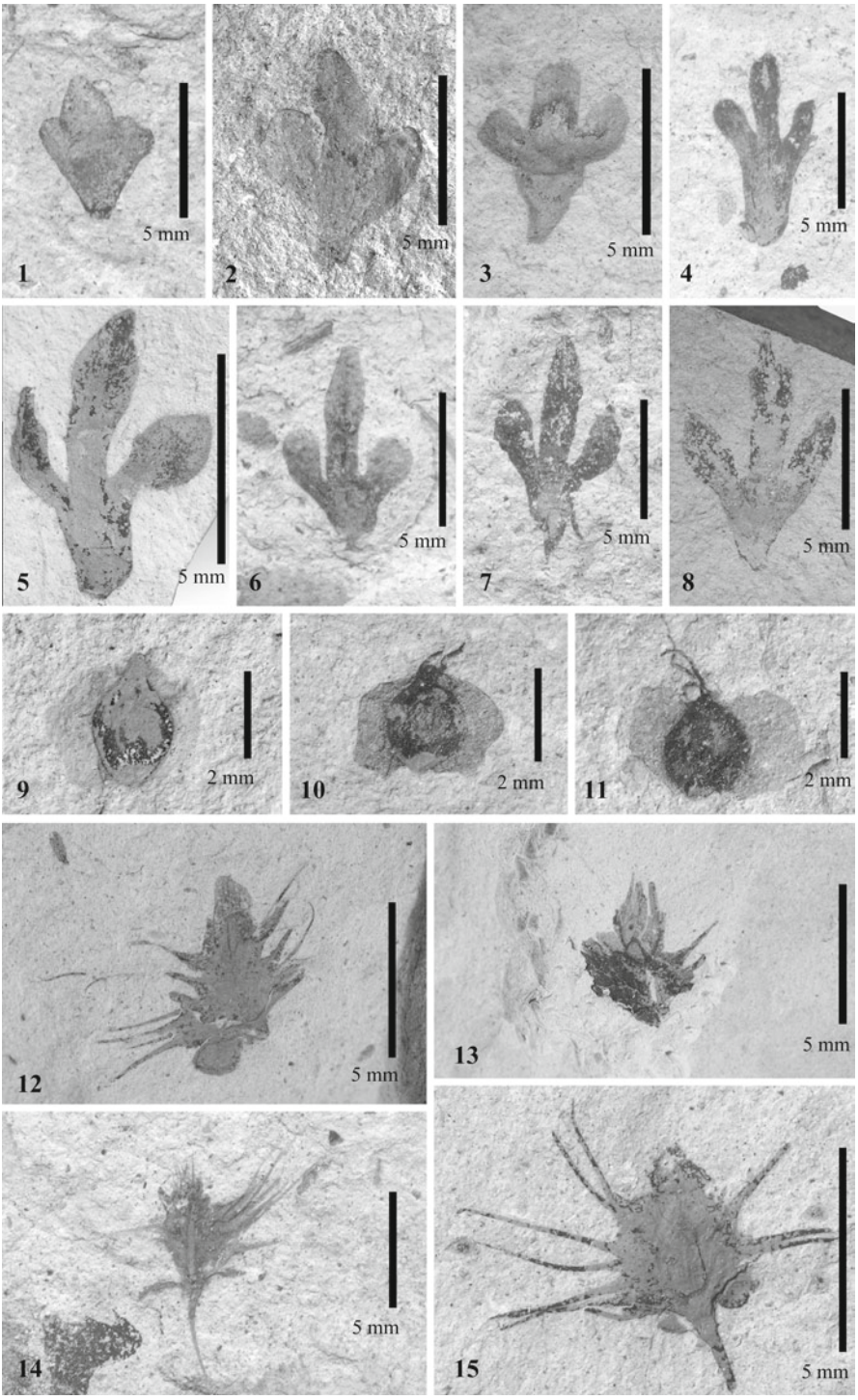

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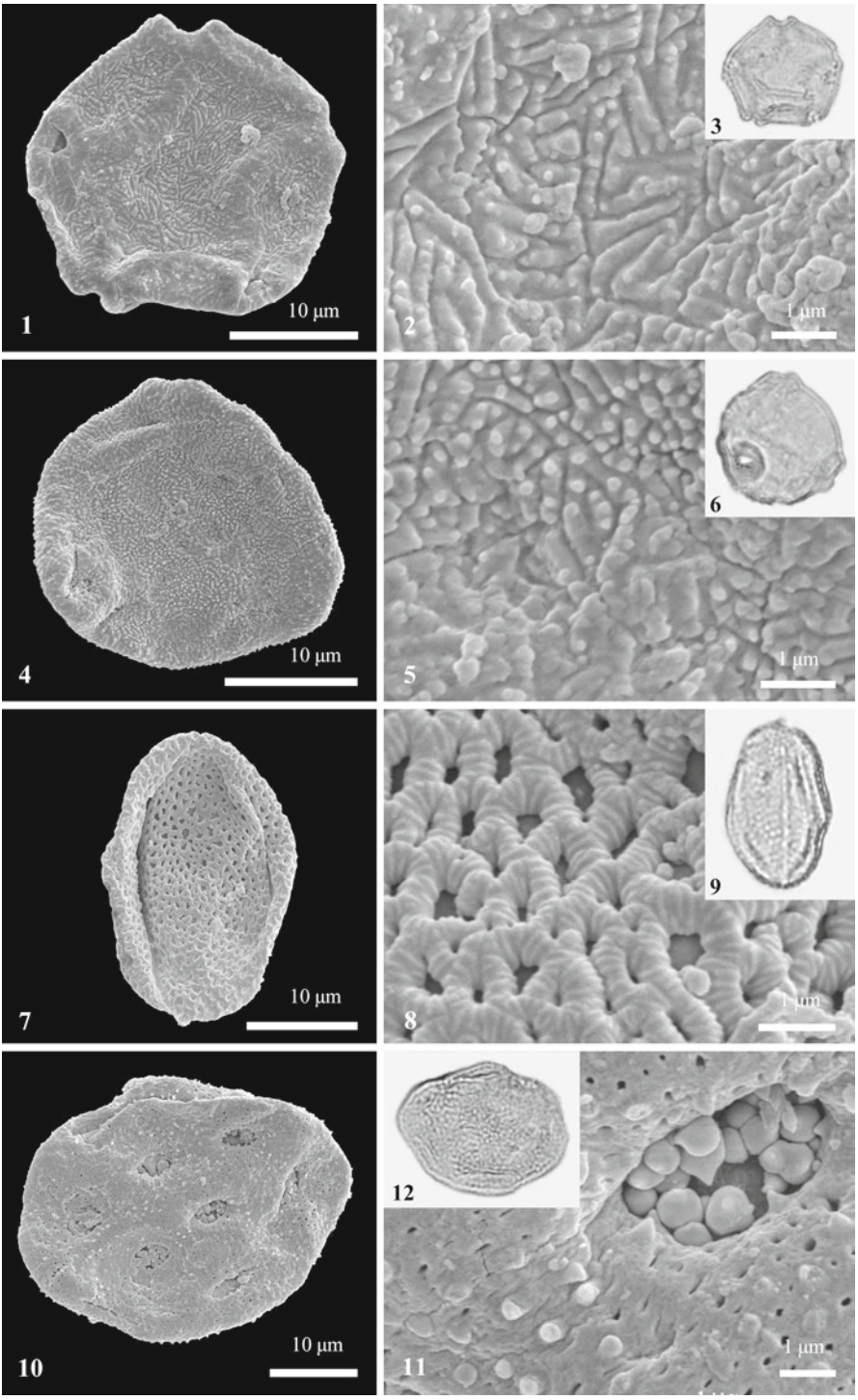



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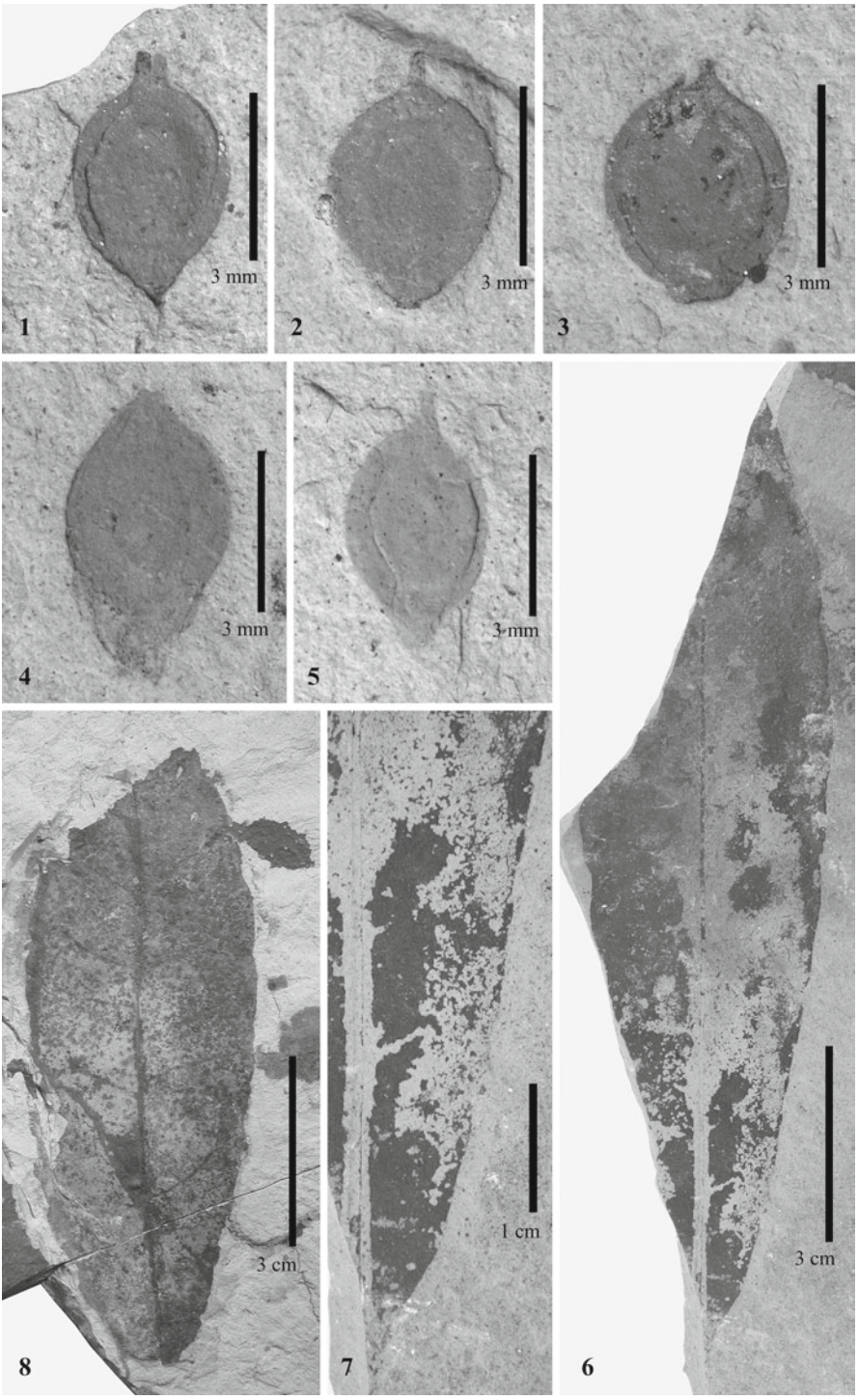



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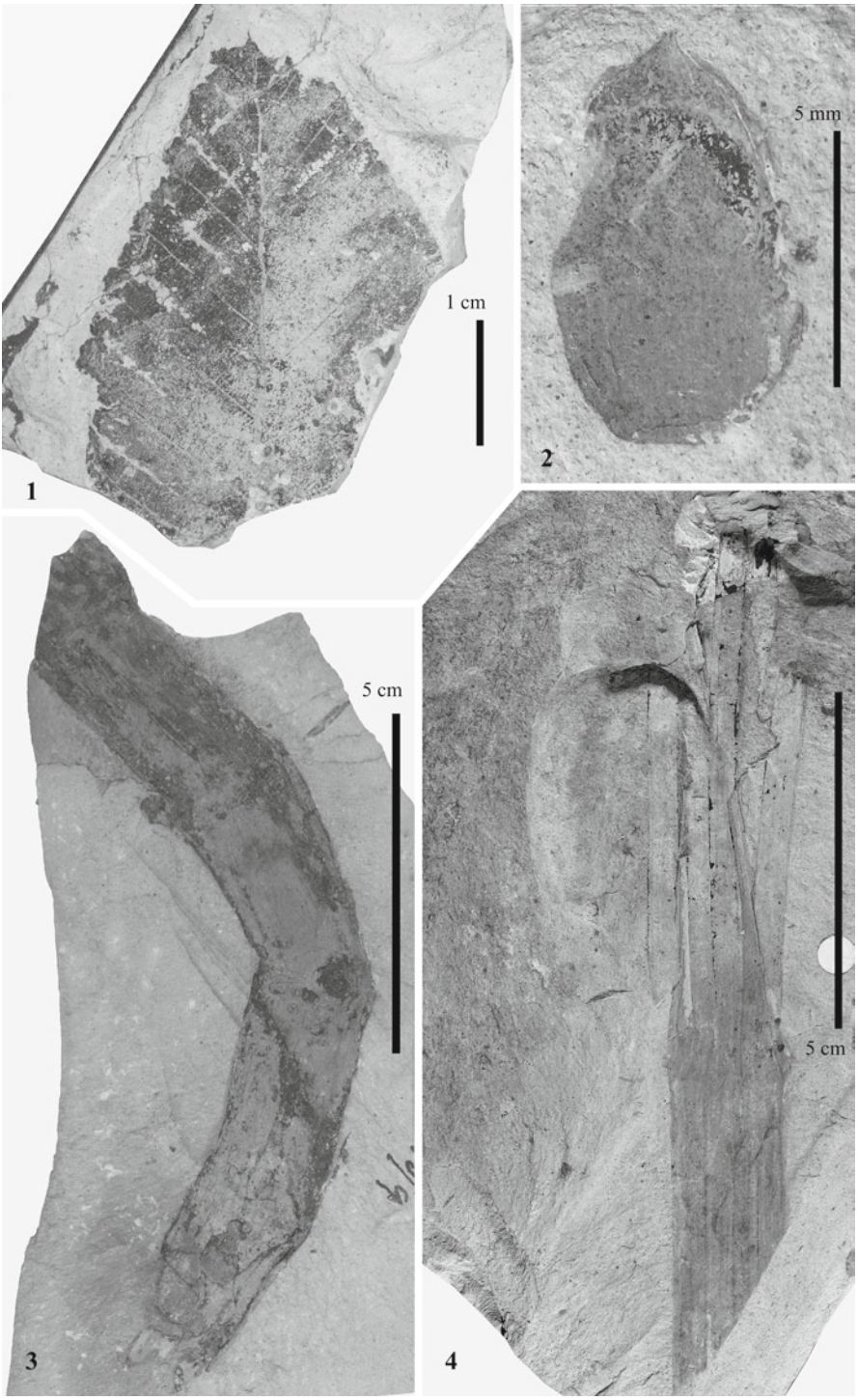



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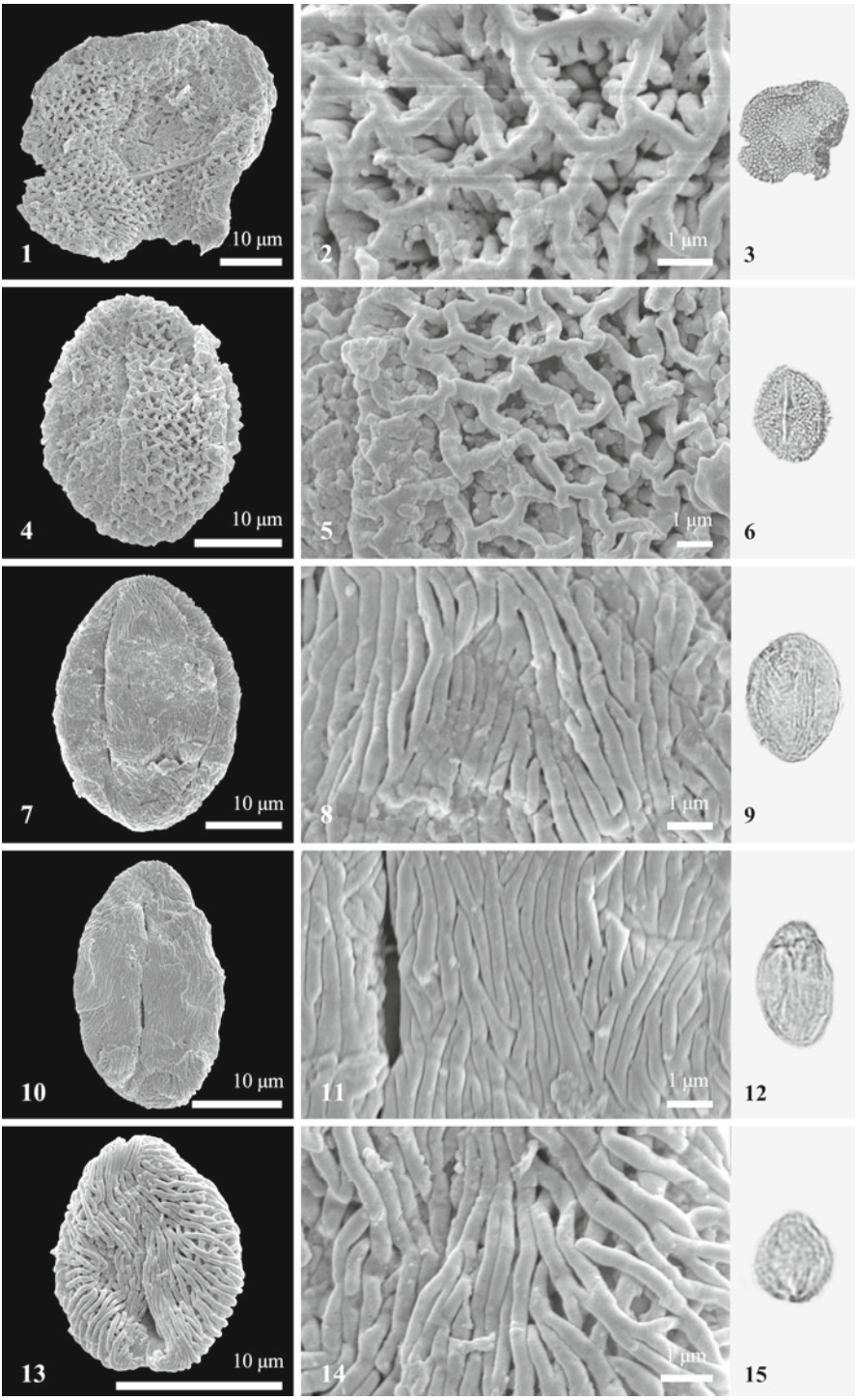

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**Plate 8.11**

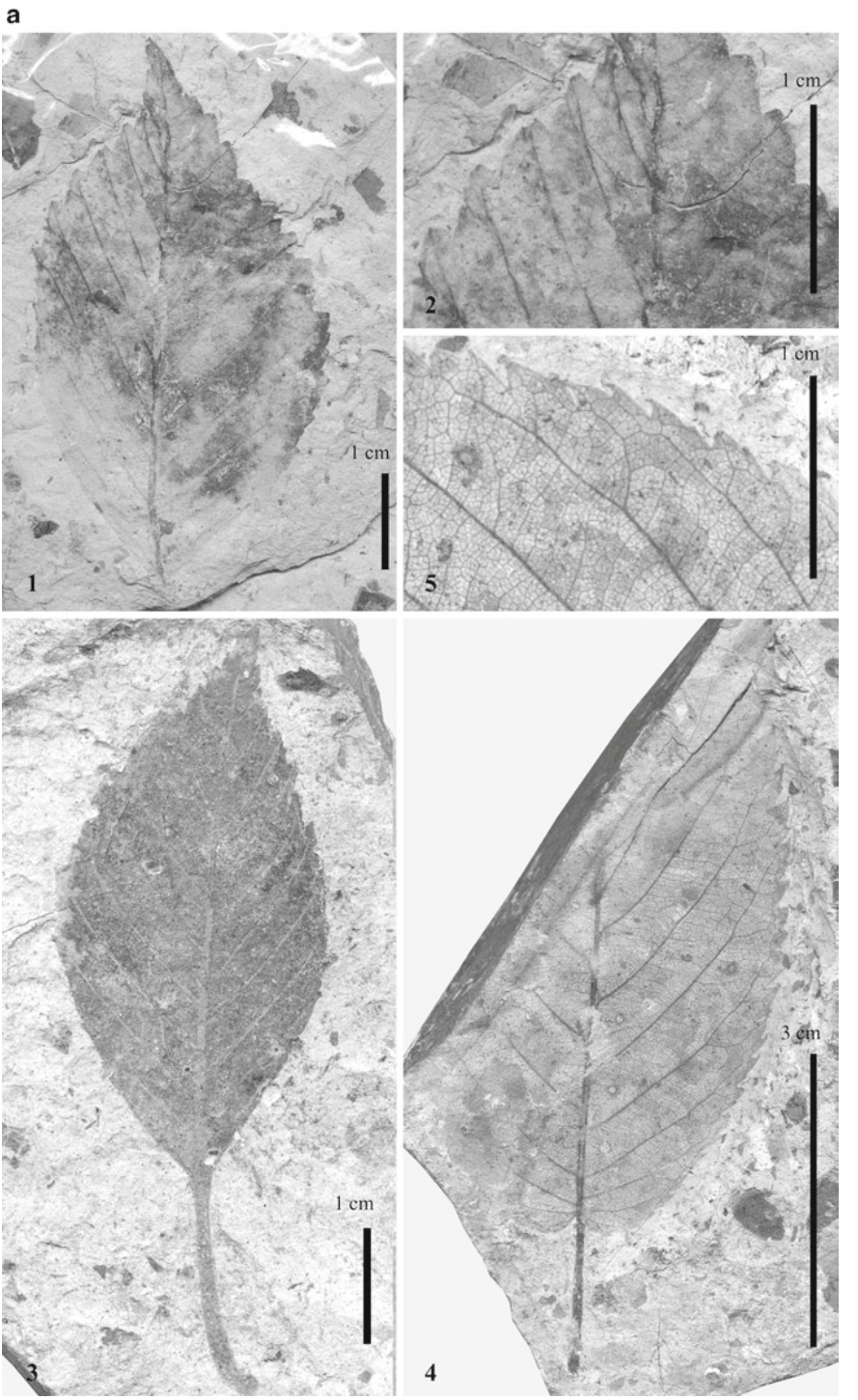



**Plate 8.12**

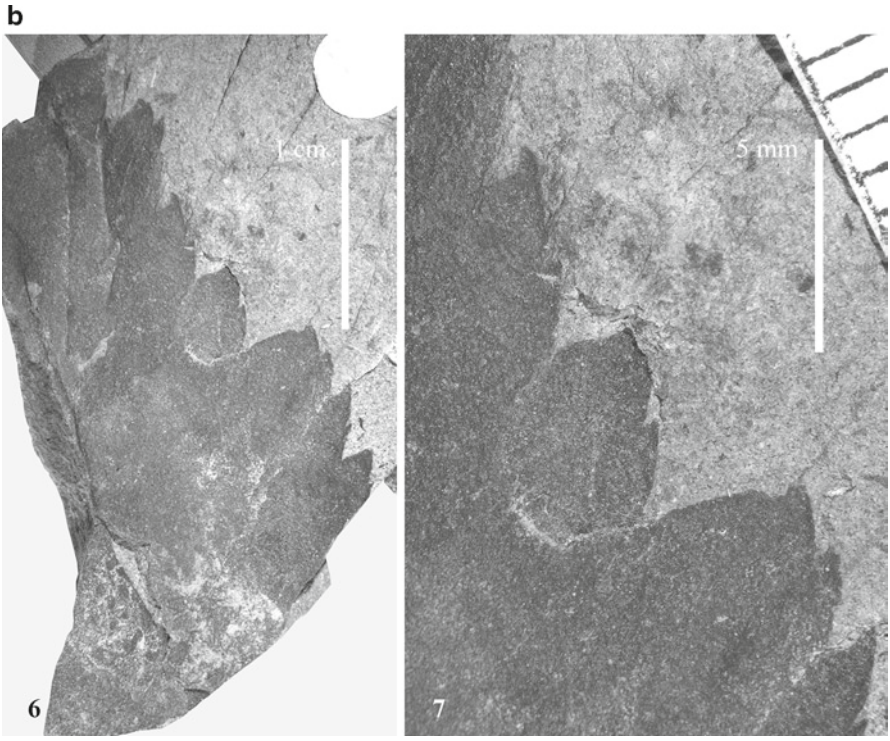



**Plate 8.12** (continued)

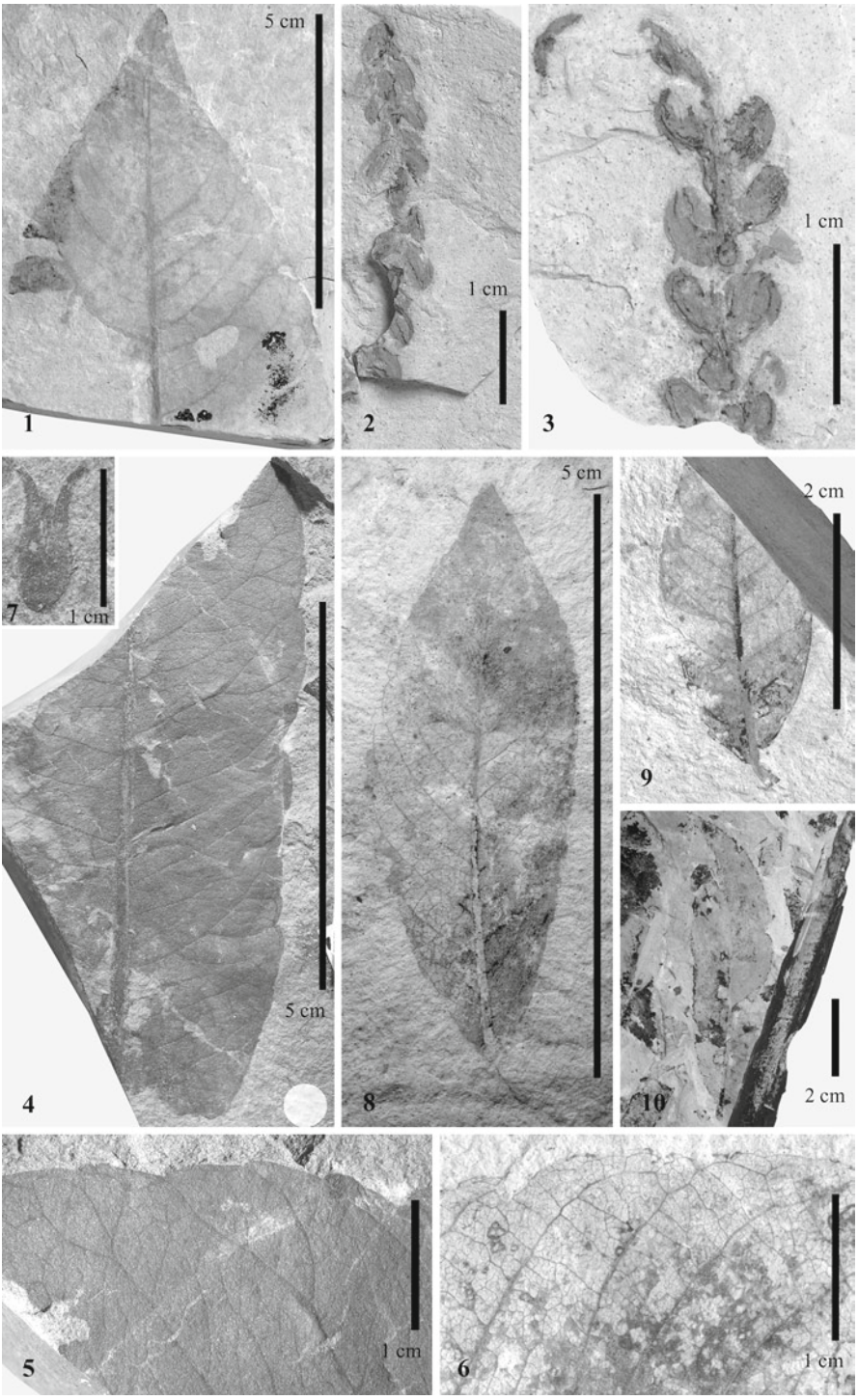



**Plate 8.13**

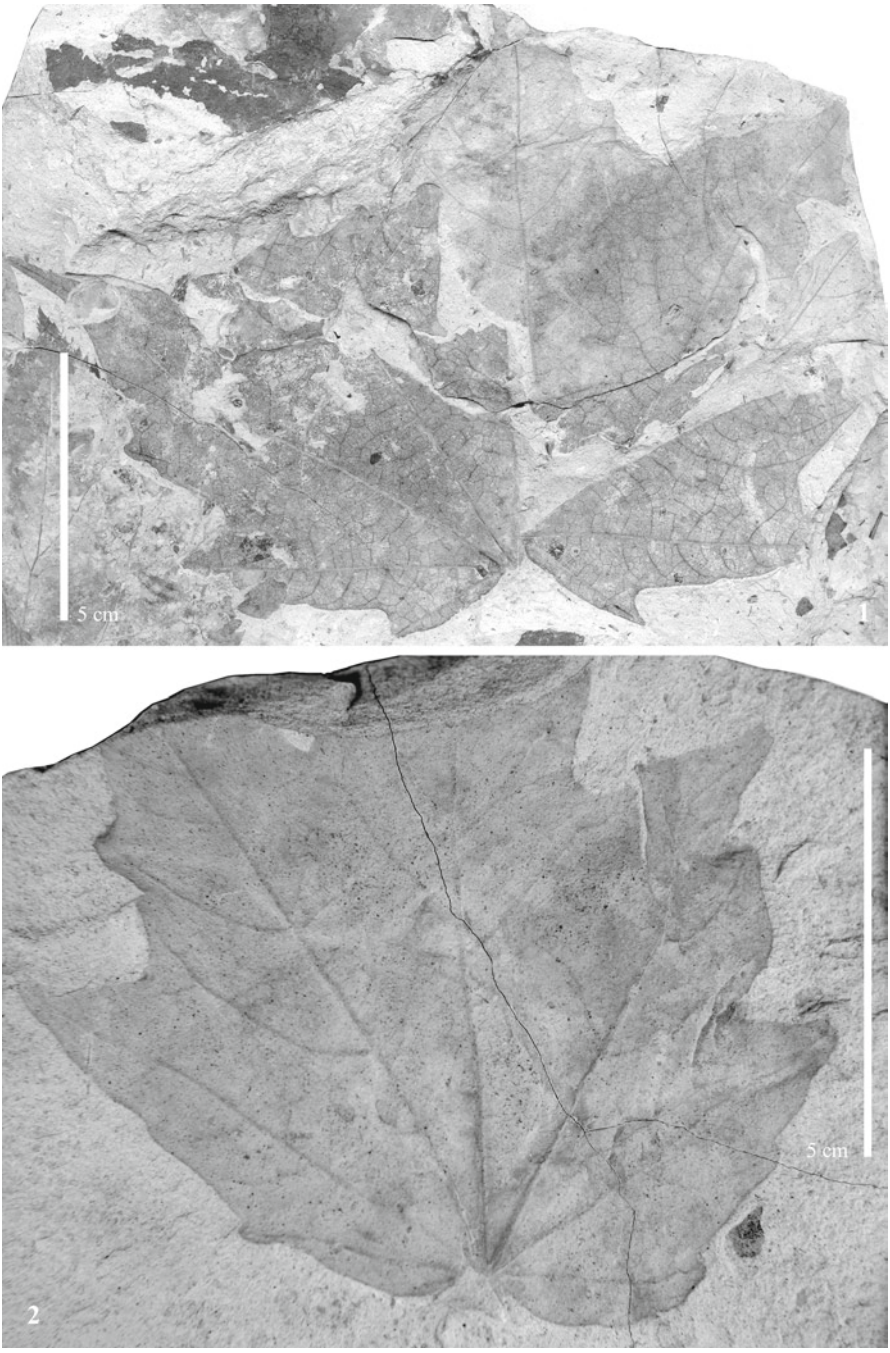



**Plate 8.14**

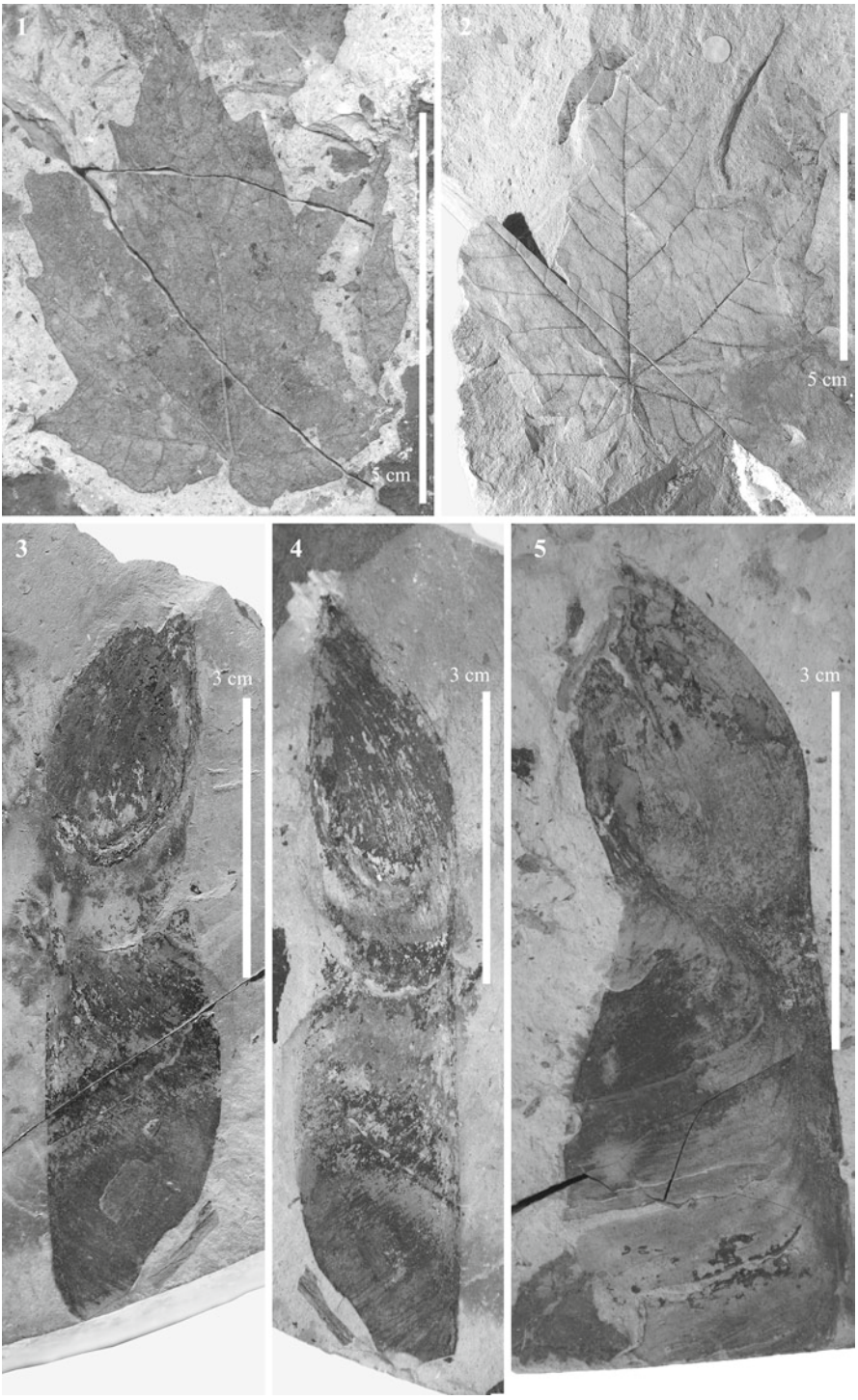



**Plate 8.15**

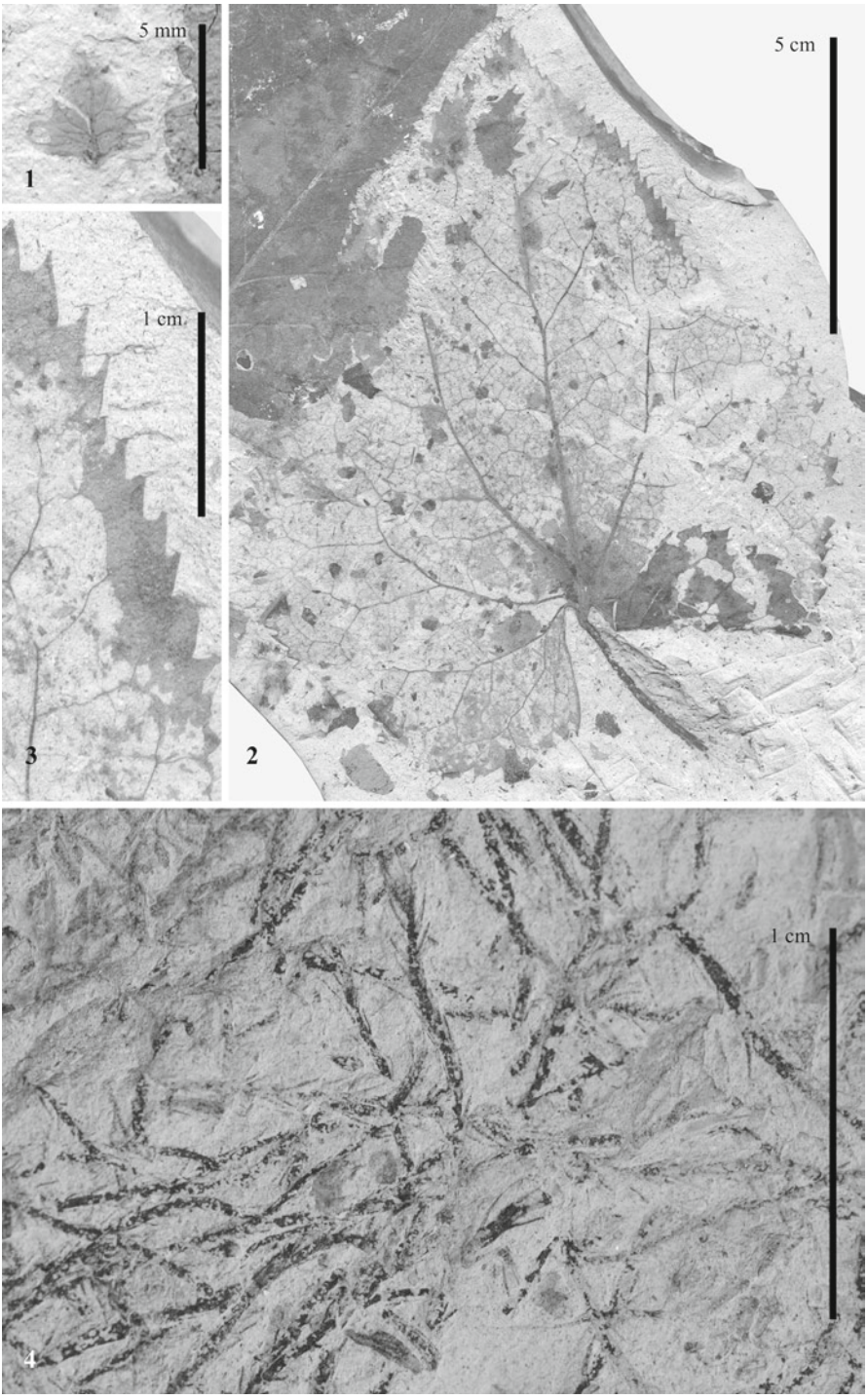



**Plate 8.16**

# Chapter 9
# A Late Messinian Palynoflora with a Distinct Taphonomy

**Abstract** A thin, white coloured ash/pumice layer on top of the poor macrofossil units at the Selárgil locality yields a rich late Messinian palynoflora that was deposited under a markedly different taphonomic setting than most other late Cainozoic floras discussed in this book. Pollen contained in this volcanic sediment apparently was deposited in a very short time during the actual ash fall, whereas in most other Cainozoic formations in Iceland pollen was deposited in clastic sediments over a longer time interval. The unusual taphonomy of the Selárgil pollen and spores assemblage possibly acted as filter against insect pollinated woody species such as *Rhododendron* subsect. *Pontica* and other tree taxa that would otherwise be expected (Juglandaceae, Ulmaceae). Overall, the arboreal flora at Selárgil contains a number of partly warmth-loving relict taxa from older formations (*Cathaya*, *Scyadopitys*, *Tetracentron*) and some newcomers (*Quercus*, two types of Ericaceae). The occurrence of a new type of *Quercus* with clear biogeographic affinities to North America points to a functioning land bridge between Iceland and Greenland during the Late Miocene and to climatic conditions in northern North America and Greenland that would have allowed for migration of oaks to Iceland.

## 9.1 Introduction

The Fnjóskadalur Formation is ca 5.5 Ma in age (late Messinian, latest Late Miocene). The sediments exposed at the Selárgil locality were first described by Pjetursson (1905). Much later, Sigurðsson (1975) gave a more complete description of the strata, including volcanic constructions, sedimentary types and structures, and origin and formation of different units. Sigurðsson also collected plant macrofossils and figured them in his work; these fossils represent the only known collection from this locality. Interestingly, from these sediments, Sigurðsson (1975) reported the first and so far only findings of freshwater bivalves from the late Cainozoic of Iceland. Around the same time, Akhmetiev et al. (1978) conducted a more regional investigation of the area and traced the occurrence of the Fnjóskadalur Formation (sediments as well as volcanic constructions). They also studied the

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macrofossils collected by Sigurðsson and the palynological content of the sediments. The pollen spectrum presented by Akhmetiev et al. (1978) is short and they reported that over 80% of the pollen was badly deformed and unidentifiable. Pflug (1959) had previously published a pollen list from these sediments but also his sample showed bad preservation and his list is rather incomplete. Based on the literature and our own studies of the macrofossils and sediments in the field it seems likely that both Pflug (1959) and Akhmetiev et al. (1978) obtained their pollen samples from the sandstone/siltstone/lignite fraction of the formation containing wood fragments and leaf impressions.

For the present study we analysed pollen from a thin white coloured ash/pumice layer close to the top of the sedimentary succession, positioned a few centimetres above the more oxidized macrofossil layers studied by previous authors. The rich and well-preserved palynoflora from the Selárgil locality contains palaeobiogeographically important elements that can be used to infer routes and modes of plant migration to Iceland during the latest Miocene.

## 9.2 Geological Setting and Taphonomy

The Fnjóskadalur Formation (5.5 Ma; Jancin et al. 1985), North Iceland (Fig. 9.1a, b) is the youngest known Miocene unit yielding plant macrofossils. The formation can be traced along valley sides of the river Fnjóská (Fig. 9.1c), from Mount Reykjafjall to the south, towards the north along the hillsides of Mount Sellandsfjall (including the Selárgil locality; Plate 9.1, 1 and 2), and past the Illugastaðir estate/church site and most of the way down the widening Fnjóskadalur valley past the Ljósavatnsskarð valley crossing (Akhmetiev et al. 1978). Sediments in this region are 25–50 m thick and composed both of clastic and volcanic units (Pjetursson 1905; Sigurðsson 1975; Akhmetiev et al. 1978). The sediments rest on eroded reversely magnetized basalts that are >6.9 Ma (Akhmetiev et al. 1978). The time span represented by the hiatus is uncertain, but basalts covering the sediments (Plate 9.1, 3–5) are between 6 and 5 Ma (Jancin et al. 1985), suggesting a ca 5.5 Ma age for the uppermost fossiliferous part of the underlying sediments.

The sedimentary rocks are mostly fluvially originated conglomerates and sandstones, with intercalated lignite and siltstone units in some areas indicating partial lake environments or at least stagnant freshwater. As in other sedimentary sequences in Iceland, a number of volcanic ash layers and tephras/tuff units are found in this formation.

The plant macrofossils at the Selárgil locality of the Fnjóskadalur Formation are badly preserved. Most of the sediments containing plant macro-remains (seen below the hammer in Plate 9.1, 5) are red or red-brownish in colour from oxidation, and the fossils are mostly found as impressions (Plate 9.1, 7–10). Faint remnants of coalified material are sometimes visible in the more brownish to greyish samples. The thin white coloured ash/pumice layer topping the macrofossil units (Plate 9.1, 6) and separating them from the fine laminated greyish siltstones just below the overlying basalt, contains no macrofossil. It does, on the other hand,

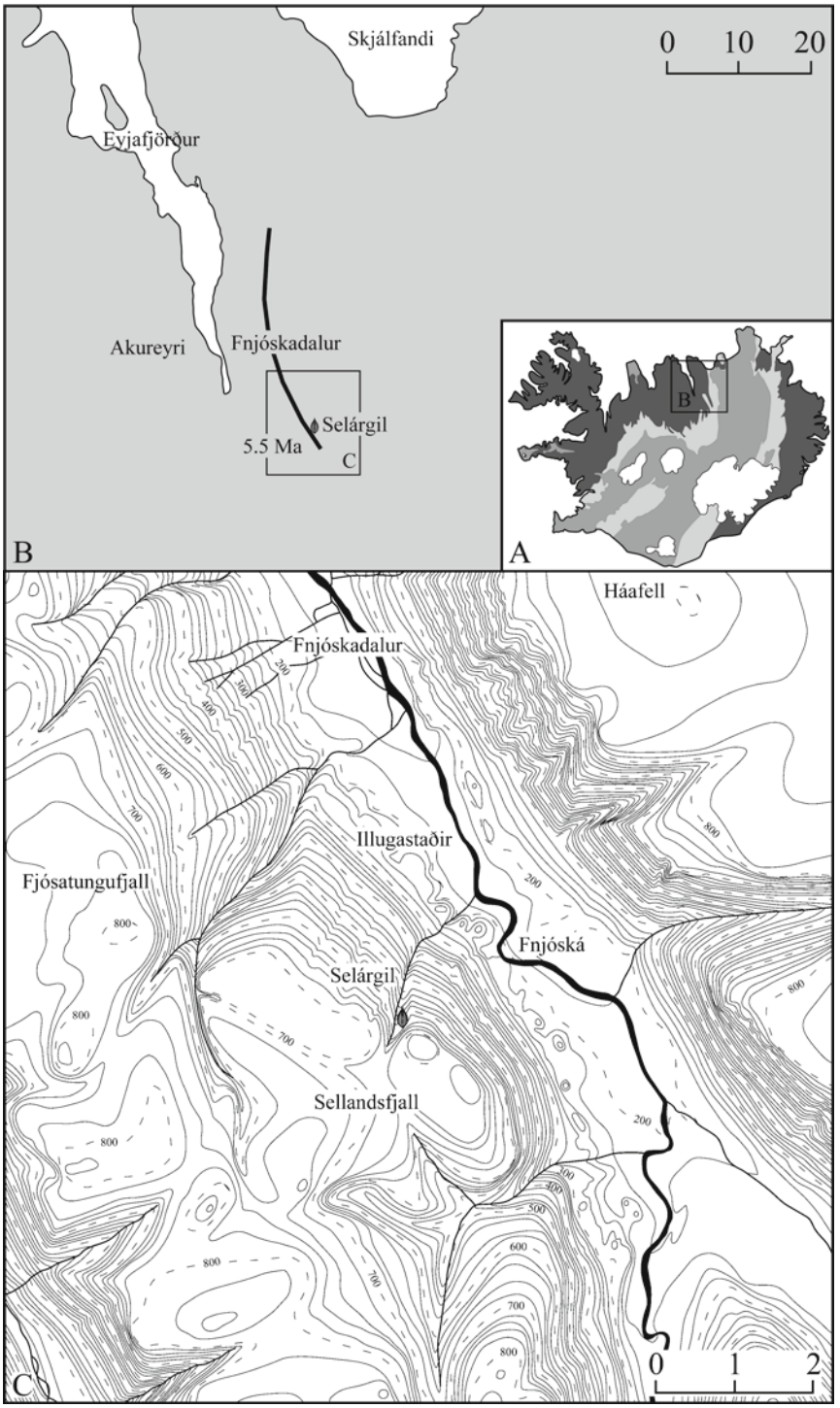



**Fig. 9.1** Map showing the fossiliferous locality of the 5.5 Ma formation. (**a**) Bedrock geology (see Fig. 1.10 for explanation), (**b**) extension of sedimentary rock formation, (**c**) Selárgil locality (Geological background modified after Jóhannesson and Sæmundsson 1989; altitudinal lines from Landmælingar Íslands 1990)

yield an exceptionally well-preserved palynoflora. Pollen is not abundant in this sample but the preservation is good. Similar excellent preservation was also noticed in the volcanic white ash fall sediments of the 10 Ma sedimentary formation (Tröllatunga locality, see Chap. 6). Interestingly, pollen in the Tertiary formations of Iceland seems to preserve fairly well in very fine ash layers of acid origin (with high silica content) but shows a much worse preservation in the more basic (low silica content) units. It seems likely that pollen contained in this volcanic layer was airborne in the Selárgil region during the actual ash fall and reflects a rather short time interval (few hours, a day to few days) of deposition compared to several of the clastic palynological samples discussed in this book which mostly represent a much longer time interval spanning some years. This might be the reason why several taxa to be expected, such as Juglandaceae, Ulmaceae, etc., were not found in this sample although they occur in both older and younger sediments. Akhmetiev et al. (1978) report some of these taxa (for example, Juglandaceae) in their clastic palynological sample of Selárgil.

## 9.3 Flora, Vegetation, and Palaeoenvironments

The late Messinian flora of Selárgil comprises 53 taxa (Table 9.1, Plates 9.2–9.20) of which by far the most are herbaceous angiosperms (27 taxa; Fig. 9.2). Mosses, ferns and fern allies are represented by seven taxa. Among trees, conifers make up six species and angiosperms ten. Three taxa belong to *incertae sedis*.

Despite the potential taphonomic bias seen in this flora (see above), the vegetation at Selárgil was diverse including wetlands, meadows and well drained lowland and montane forests (Table 9.2, Fig. 9.3). Lowlands were covered by wetlands, rich meadows and shrublands (Fig. 9.4). Stagnant water provided habitats for water plants (*Myriophyllum, Nuphar, Menyanthes*) and was surrounded by swamp vegetation comprising herbaceous plants and woody shrubs and trees (Ericaceae, *Alnus*). More closed backswamp forests were probably dominated by *Alnus* and species of *Salix*. Well-drained lowland forests including levées and lake margins might have been more diverse in woody species and comprised mixed stands of Betulaceae, *Quercus* and *Salix*. Conifers may have been rare elements in the foothill forests but became more abundant in the montane forests where they formed part of mixed broadleaved deciduous and conifer forests (Fig. 9.5). Overall, conifers were quite diverse and may have had different ecologies. For example, *Cathaya*, which had its last occurrence in Iceland during the deposition of the Fnjóskadalur Formation might have thrived in microclimatically favoured areas, such as humid ravine-like forests, while some others, such as *Pinus* and *Larix*, were possibly components of various forest types. Also herbaceous taxa occupied different niches (Table 9.2) as is also seen in the modern vegetation of Iceland. In general, palaeobotanical evidence suggests a typical cool temperate, rather humid, appearance for the late Messinian vegetation in Iceland. A few exotic woody elements persisted from the older floras (*Cathaya*, *Sciadopitys*, *Tetracentron*).

**Table 9.1** Taxa recorded for the 5.5 Ma floras of Iceland

| Fnjóskadalur Formation 5.5 Ma<br>Taxa | Pollen | Leaves | RP | Other | DM |
|---|---|---|---|---|---|
| Bryophyta | + | | | | 1a |
| *Sphagnum* sp. | | | | | |
| Equisetaceae | | | | | |
| *Equisetum* sp. | | | | + | 1a |
| Lycopodiaceae | | | | | |
| *Lycopodium* | + | | | | 1a |
| Polypodiaceae | | | | | |
| Polypodiaceae gen. et spec. indet. 1 | + | | | | 1a |
| Polypodiaceae gen. et spec. indet. 7 | + | | | | 1a |
| Polypodiaceae gen. et spec. indet. 8 | + | | | | 1a |
| Incertae sedis – unassigned spores | | | | | |
| Trilete spore, fam., gen. et spec. indet. 2 | + | | | | 1a |
| Pinaceae | | | | | |
| *Abies steenstrupiana* | + | | + | | 2a |
| *Cathaya* sp. | + | | | | 2a |
| *Picea* sect. *Picea* | + | + | | | 2a |
| *Pinus* sp. 1 (Diploxylon type) | + | | | | 2a |
| *Pseudotsuga/Larix* sp. | + | | | | 2a |
| Sciadopityaceae | | | | | |
| *Scyadopitys* sp. | + | | | | 2a |
| Apiaceae | | | | | |
| Apiaceae gen. et spec. indet. 6 | + | | | | 1b |
| Apiaceae gen. et spec. indet. 7 | + | | | | 1b |
| Asteraceae | | | | | |
| *Artemisia* sp. 2 | + | | | | 1a |
| Asteraceae gen. et spec. indet. 1 | + | | | | 1a |
| Asteraceae gen. et spec. indet. 2 | + | | | | 1a |
| Asteraceae gen. et spec. indet. 4 | + | | | | 1a |
| Betulaceae | | | | | |
| *Alnus cecropiifolia* | + | + | | | 1a, 2a |
| *Betula cristata* | (+) | + | | | 1a |
| *Betula* sp. A (section *Betulaster*) | (+) | + | | | 1a |
| Calycanthaceae | | | | | |
| aff. Calycanthaceae | + | | | | 1b |
| Caryophyllaceae | | | | | |
| Caryophyllaceae gen. et spec. indet. 4 | + | | | | 1b |
| Ericaceae | | | | | |
| Ericaceae gen. et spec. indet. 2 | + | | | | 1b |
| Ericaceae gen. et spec. indet. 3 | + | | | | 1b |
| Fagaceae | | | | | |
| *Quercus* infrageneric group *Quercus* sp. 2 | + | | | | 2b, 3 |
| Haloragaceae | | | | | |
| *Myriophyllum* sp. 1 | + | | | | 1b |

(continued)

**Table 9.1** (continued)

| Fnjóskadalur Formation 5.5 Ma<br>Taxa | Pollen | Leaves | RP | Other | DM |
|---|---|---|---|---|---|
| Liliaceae | | | | | |
| Liliaceae gen. et spec. indet. 4 | + | | | | 2a |
| Menyanthaceae | | | | | |
| *Menyanthes* sp. | + | | | | 1b |
| Nymphaceae | | | | | |
| *Nuphar* sp. | + | | | | 1b |
| Plantaginaceae | | | | | |
| aff. *Plantago lanceolata* | + | | | | 1b |
| Poaceae | | | | | |
| *Phragmites* sp. | | | | + | 1b |
| Poaceae gen. et spec. indet. 2 | + | | | | 1b, 2a |
| Poales | | | | | |
| Poales fam., gen. et spec. indet. | | + | | + | 1b, 2a |
| Polygonaceae | | | | | |
| *Polygonum viviparum* | + | | | | 1b |
| Ranunculaceae | | | | | |
| *Ranunculus* sp. 1 | + | | | | 1b |
| *Ranunculus* sp. 2 | + | | | | 1b |
| *Thalictrum* sp. 1 | + | | | | 1b, 2a |
| Ranunculaceae gen. et spec. indet. 2 | + | | | | 1b |
| Ranunculaceae gen. et spec. indet. 3 | + | | | | 1b |
| Rosaceae | | | | | |
| *Sanguisorba* sp. | + | | | | 1b, 2a |
| Rosaceae gen. et spec. indet. 10 | + | | | | 1b |
| Rosaceae gen. et spec. indet. 11 | + | | | | 1b |
| Rosaceae gen. et spec. indet. 12 | + | | | | 1b |
| Salicaceae | | | | | |
| *Salix gruberi* | (+)2 | **+** | | | 1a |
| *Salix* sp. A | (+)2 | + | | | 1a |
| Sparganiaceae | | | | | |
| *Sparganium* sp. | **+** | | | | 1b |
| Trochodendraceae | | | | | |
| *Tetracentron atlanticum* | + | | | | 2a |
| Valerianaceae | | | | | |
| aff. *Valeriana* sp. | + | | | | 1a |
| Incertae sedis – Magnoliophyta | | | | | |
| Pollen type 21 | + | | | | ? |
| Pollen type 22 | + | | | | ? |
| Pollen type 23 | + | | | | ? |

*L* leafy axis, *A* fruit attached to leafy axis, *D* fruit dispersed, *RP* reproductive structure, + organ present, **+** original description of species based on this organ, (+) organ belonging to genus but uncertain to which of the species, (+) 2 indicating number of pollen types possibly belonging to the eponymous morphotaxon, *DM* dispersal mode: *1a* wind long distance (anemochory), *1b* bird long distance (endozoochory), *2a* wind short distance (anemochory), *2b* animals short distance (exozoochory), *3* dyschory

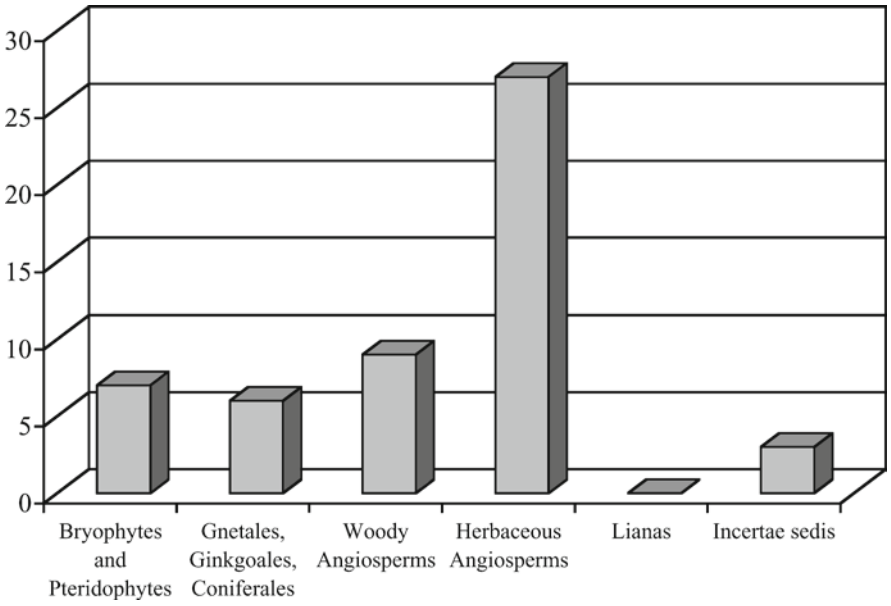



**Fig. 9.2** Distribution of life forms and higher taxa among the plants recovered from the 5.5 Ma sedimentary rock formation. Height of columns indicates number of taxa

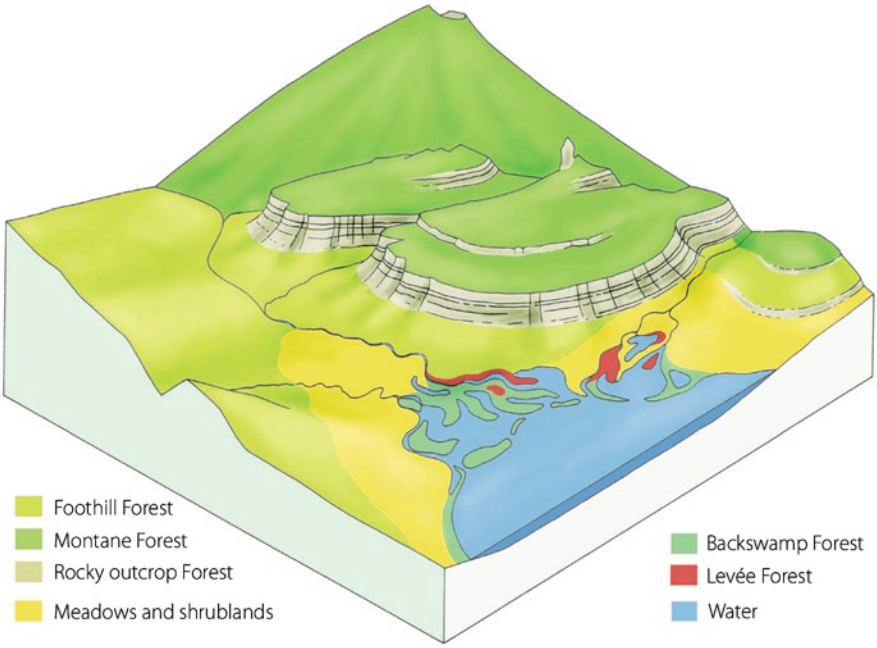



**Fig. 9.3** Schematic block diagram showing palaeo-landscape and vegetation types for the late Late Miocene of Iceland. See Table 9.1 for species composition of vegetation types

**Table 9.2** Vegetation types and their components during the late Messinian

| **Vegetation types 5.5 Ma** | | | |
|---|---|---|---|
| **Aquatic vegetation** | **Backswamp forests and temporally flooded lake margin** | **Foothill forests** | *Betula* sp. A |
| *Equisetum* sp. | *Equisetum* sp. | Polypodiaceae gen. et spec. indet. 1, 7, 8 | Caryophyllaceae gen. et spec. indent. 4 |
| *Myriophyllum* sp. 1 | Polypodiaceae gen. et spec. indet. 1, 7, 8 | *Alnus cecropiifolia* | Ericaceae gen. et spec. indet. 2, 3 |
| Liliaceae gen. et spec. indet. 4 | Apiaceae gen. et spec. indet. 6, 7 | *Betula cristata* | *Plantago lanceolata* type |
| *Menyanthes* sp. | *Alnus cecropiifolia* | *Betula* sp. A | Poaceae gen. et spec. indet. 2 |
| *Nuphar* sp. | aff. Calycanthaceae | *Quercus* sp. 2 | *Polygonum viviparum* |
| *Phragmites* sp. | Poaceae gen. et spec. indet. 2 | | *Ranunculus sp. 1, 2* |
| *Sparganium* sp. | *Salix* sp. A | **Montane forests** | *Thalictrum sp. 1* |
| | Valerianaceae aff. *Valeriana* sp. | *Abies steenstrupiana* | Ranunculaceae gen. et spec. indet. 2, 3 |
| **Swamp vegetation** | | *Cathaya* sp. | *Sanguisorba* sp. |
| *Sphagnum* sp. | **Levée forests, well-drained lowland forests and lake margins** | *Picea* sp. | Rosaceae gen. et spec. indet. 10–12 |
| *Equisetum* sp. | Polypodiaceae gen. et spec. indet. 1, 7, 8 | *Pinus* sp. 1 | Valerianaceae aff. *Valeriana* sp. |
| Apiaceae gen. et spec. indet. 6, 7 | *Alnus cecropiifolia* | *Larix* sp. | |
| *Alnus cecropiifolia* | *Betula cristata* | *Sciadopitys* sp. | **Rocky outcrop forests** |
| Ericaceae gen. et spec. indet. 2, 3 | aff. Calycanthaceae | *Betula* sp. A | *Lycopodium* sp. |
| Liliaceae gen. et spec. indet. 4 | *Quercus* sp. 2 | *Tetracentron atlanticum* | *Pinus* sp. 1 |
| *Menyanthes* sp. | *Salix* sp. A | | *Larix* sp. |
| Poaceae gen. et spec. indet. 2 | Valerianaceae aff. *Valeriana* sp. | **Meadows and shrublands** | *Plantago lanceolata* type |
| Poales fam. gen. et spec. indet. | | *Sphagnum* sp. | Poaceae gen. et spec. indet. 2 |
| *Sparganium* sp. | | *Equisetum* sp. | *Polygonum viviparum* |
| | | *Lycopodium* sp. | *Thalictrum* sp. 1 |
| | | Apiaceae gen. et spec. indet. 6, 7 | *Sanguisorba* sp. |
| | | *Artemisia* sp. 2 | Rosaceae gen. et spec. indet. 10–12 |
| | | *Asteraceae* gen. et spec. indet. 1, 2, 4 | *Tetracentron atlanticum* |
| **AZONAL VEGETATION** | | **ZONAL VEGETATION** | |

The palaeoecology of fossil species is reconstructed from their sedimentological context and ecology of modern analogues

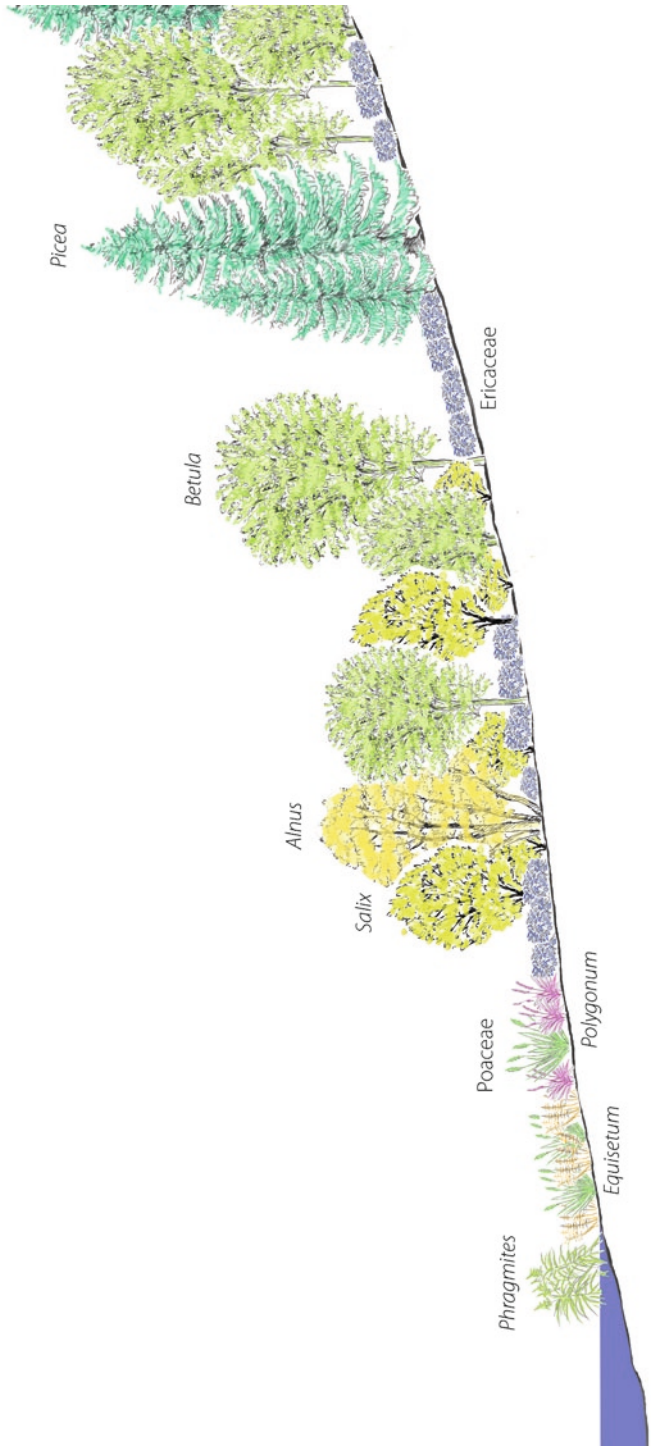



**Fig. 9.4** Schematic transect of a lake margin with moist meadows changing into a light forest dominated by Betulaceae and *Salix*

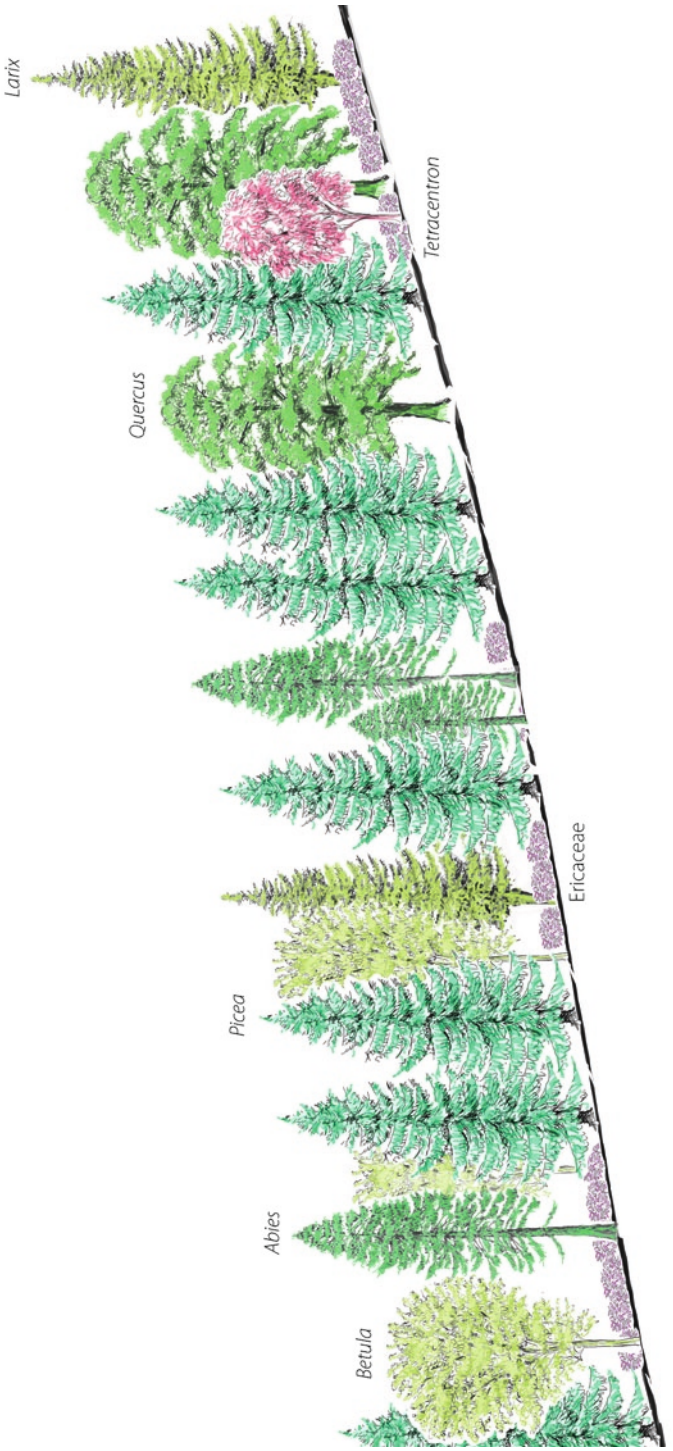



**Fig. 9.5** Schematic transect showing of well-drained foothill and montane forest dominated by conifers with admixture of *Quercus*

## 9.4 Climatic Requirements of Some Potential Modern Analogues

*Cathaya* is endemic to central South China (Flora of China Editorial Committee 1999) where it thrives in humid areas between 900 and 1,900 m a. s. l. with MAT 9.3–18.6°C (Cfa climate; Kottek et al. 2006). It typically occurs on slopes and open ridges in connection with mixed mesophytic and broad leaved evergreen forests. Clearly, this genus had a much wider distribution in the past (Liu and Basinger 2000) and persisted in Europe until the Pleistocene. Hence, it may have extended well into cooler variants of humid temperate climate types (Cfb, Cfc climates).

Apart from *Cathaya*, *Sciadopitys* is the most warmth-loving element among the conifers. At present, *Sciadopitys* is a monotypic genus (see Chap. 5) confined to cool-temperate, mixed evergreen-deciduous forests, often in pure stands. It thrives in a Cfa to Dfb (snow, fully humid with warm summers; Köppen and Geiger 1928; Kottek et al. 2006) climate with MAT 7.4–16.6°C (temperature range from Utescher & Mosbrugger 2009).

*Tetracentron* (Trochodendraceae) is a monotypic genus with only one living species, *Tetracentron sinense* Oliv. restricted to central and southwestern China, northern Vietnam, northern Burma, and south of the Himalayas to northeastern India, Bhutan, and eastern Nepal. *Tetracentron* occurs along streams and forest margins in broadleaved evergreen forests and mixed evergreen-deciduous forests at elevations between 1,100 and 3,500 m a. s. l. (Fu and Bartholomew 2001). It thrives under a variety of climate types (Cfa, Cfb, Cwa, Cwb, Cwc, Dfb; Kottek et al. 2006) with MAT ranging from ca 2.2°C to 19°C. This genus is unambiguously recorded from Icelandic sediments based on diagnostic pollen, fruits, and leaves. It has a stratigraphic range from 15 to 3.6 Ma (see Chap. 12). Another element with a long stratigraphic record is pollen with clear affinities to Calycanthaceae that occur in a similarly wide range of climate types.

*Quercus* is represented by a distinct type of pollen that shows systematic affinities with extant white oaks (infrageneric group *Quercus*) and red oaks (infrageneric group *Lobatae*; Denk et al. 2010). Among these groups, the observed vermiculate tectum ornamentation appears to be confined to North American species (Solomon 1983a, b). Among modern oaks, white oaks and red oaks have the most northern and most continental distribution (Camus 1936–1938, 1938–1939, 1952–1954). Red oaks have their centre of diversity in Mexico and Central America but some species can cope with cool temperate climates with winter frosts. The widespread eastern North American *Q. rubra* L., for example, occurs in humid temperate (Cfa, Cfb, Cfc) and snow (Dfa, Dfb, Dfc) climate types; Kottek et al. 2006) with MAT ranging from −1.1°C to 19.4°C (Thompson et al. 1999). White oaks have a similar range as red oaks in North America but extend even further into cold continental areas with severe winter frosts (Jensen 1997; Nixon and Muller 1997). *Quercus macrocarpa* Michx. is native to the eastern and mid-western United States and Canada and grows under MAT −1.5°C to 21.8°C (Thompson et al. 1999).

The bulk of taxa recorded for the 5.5 Ma formation is not indicative of a particular climate type but rather indifferent and able to thrive in cool and warm temperate climates including snow climates.

## 9.5 Taxonomic Affinities and Origin of Newcomers

The most spectacular newcomer in the ca 5.5 Ma flora of Iceland is *Quercus* morphotype 2 with clear affinities to North American white or red oaks (Denk et al. 2010).

In North America, red and white oaks extend into areas with MAT below the freezing point and with severe frosts during the winter (see above). Although there is convincing evidence for the formation of glaciers in southern Greenland during the Miocene, these glaciers were confined to mountains at 7.3 Ma (St. John and Krissek 2002), and large-scale northern hemispheric glaciations started not earlier than at the Pliocene-Pleistocene boundary (ca 2.7 Ma, Gibbard and Cohen 2009; East Norwegian-Greenland Sea and Barents Sea [Thiede et al. 1998]; 2.8–2.7 Ma Vøring Plateau [Fronval and Jansen 1996]; 2.8–2.6 Ma, Iceland [Geirsdóttir and Eiríksson 1994]; 3.5–2.7 Ma, Greenland [St. John and Krissek 2002]). Plant fossil evidence indicates that Iceland had a warm temperate Cfa climate until at least 12 Ma, and a cool temperate Cfb/Cfc climate suitable for white and/or red oaks until ca 3.6 Ma (see Chap. 13). In view of glaciers of varying size on the mountains of southern Greenland in the Late Miocene and the absence of large-scale ice sheets until the latest Early Pliocene (St. John and Krissek 2002), white and red oaks appear ecologically suited to have colonized Iceland via Greenland from North America during the latest Miocene (ca 6 Ma). Assuming that there is no sampling bias, this type of oak would have migrated to Iceland between 8 and 5.5 Ma (Denk et al. 2010). During the Pliocene and parts of the Early Pleistocene the Earth experienced phases of markedly warm climates. First, between ca 4.5 and 2.7 Ma (Haug et al. 2004), the Mid-Pliocene Climatic Optimum caused conditions in the northern North Atlantic and the Arctic Ocean east of Greenland with summer sea surface temperatures up to >8°C warmer than today (Robinson 2009). In the Early Pleistocene, forest tundra extended to northern Greenland and Bennike (1990) estimated summer temperatures 7–8°C warmer than today. This warming occurred after the first large-scale glaciations in this region (see above) and caused the Inland Ice of Greenland to melt (Bennike 1990). Given such warm conditions in the northern part of Greenland during various times in the later Neogene it appears to be plausible that the link between Greenland and North America via Queen Elizabeth Island may have been passable at the time, when *Quercus* morphotype 2 migrated to Iceland. This is the last record for the migration of short-distance dispersed plants from the west to Iceland.

Among woody plants, two distinct types of Ericaceae tetrads occur for the first time in Iceland in the 5.5 Ma formation (cf. Table 9.2). No closer taxonomic and biogeographic affinities can be established for these types at the moment. The remaining newcomers are widespread cosmopolitan herbaceous taxa with long-distance dispersal and unidentified angiosperms.

## 9.6 Comparison to Coeval Northern Hemispheric Floras

The Late Miocene Lava Camp flora and insect fauna (ca 5.7±0.2 Ma) from the Bering Strait region was described by Hopkins et al. (1971) and Matthews and Ovenden (1990). The flora is dominated by *Larix* leaves and short shoots. Among the conifers, a member of *Pinus* subsection *Cembrae* with a modern Eurasian distribution is noteworthy. The remaining conifer taxa are closely related to species that are at present endemic to northwestern North America (*Picea mariana* (Mill.) Britton, Sterns & Poggenb., *P. glauca* (Moench) Voss, *P. sitchensis* (Bong.) Carrière, *Tsuga heterophylla* (Raf.) Sarg., *T. mertensiana* (Bong.) Carrière; Appendix 9.1). In addition, Hopkins et al. (1971) compared cupressaceous pollen to *Chamaecyparis* that grows as far north as southern Alaska today. Compared to the Icelandic Selárgil flora, the Lava Camp flora was clearly dominated by conifers and, not surprisingly, had closer biogeographic affinities to western North America and Eastern Asia (the Bering land bridge was active until ca 5.5–4.8 Ma; Marincovich and Gladenkov 1999). For the insect assemblage found at Lava Camp, Hopkins et al. (1971) concluded that at present such a fauna could possibly be found in southern British Columbia or northern Washington but not on the modern tundra of Seward Peninsula or in the boreal woodlands of interior Alaska. Today, British Columbia and the northern parts of Washington have humid variants of a Cfb (to Csb) climate, whereas the Bering Strait region (Russian and Alaskan parts) has Dfc (for example, Nome, Alaska, Lieth et al. 1999) or ET climates (Mys Uelen, Russia; Barrow, Alaska; Lieth et al. 1999).

In Central Europe, the flora of Murat has been absolutely dated as ca 5.3 Ma (Roiron 1991; Appendix 9.1). This flora is dominated by broadleaved deciduous angiosperms with an admixture of conifers. While most of the genera present in the flora of Murat were also present in the Middle Miocene floras of Iceland (cf. Chaps. 4 and 5), a number of taxa have never been reported from Iceland (*Bambusa, Berberis, Cedrela, Celtis, Zelkova*). According to Roiron (1991), the lack of Lauraceae, *Fagus*, *Liquidambar*, and *Platanus*, among others, in the flora of Murat along with the greater abundance of temperate and cool elements compared to slightly older floras from the French Massif Central point to a climate cooling in the latest part of the Miocene.

## 9.7 Summary

The Selárgil palynoflora recovered from a thin white coloured ash/pumice layer close to the top of the Fnjóskadalur Formation is ca 5.5 Ma in age. Unlike most other floras from Cainozoic sediments of Iceland, the palynoflora of Selárgil most probably was deposited during a single volcanic eruption. The palynomorphs recorded point to a cool temperate climate (Cfb sensu Köppen) providing suitable conditions for a number of warm-loving relict taxa from older floras of Iceland. Similar warm conditions have been inferred from well-dated more or less coeval sediments in the Bering Strait region that yielded rich plant and insect assemblages. The first appearance in Iceland of a distinct type of *Quercus* with clear North

American biogeographic affinities also indicates that the Greenland-Iceland portion of the North Atlantic Land Bridge was functioning during the Late Miocene. This assumption is based on the fact that acorns of *Quercus* are not dispersed over long distances by wind or birds. In addition, a Late Miocene migration of *Quercus* to Iceland from North America would require that suitable (climatic) habitats for oaks extended much further than the Arctic Circle and reached as far north as ca 78°N (Queen Elizabeth Islands). This appears to be plausible in view of various warm phases recorded for the later Cainozoic at high northern latitudes (Mid-Pliocene Climatic Optimum at ca 4.5–2.7 Ma; warm period at ca 2.4–2.1 Ma). During these warm periods, Arctic areas such as northern Greenland experienced conditions with summer sea surface temperatures up to 8°C warmer than today. Hence, colonization of Iceland could have been from northern North America via the Queen Elizabeth Islands, southwards along western Greenland and over a partly emerged Greenland-Iceland ridge.

## Appendix 9.1

Floristic composition of the 5.5 Ma sedimentary formation of Iceland compared to contemporaneous northern hemispheric fossil assemblages at mid and high-latitudes.

| **Fnjóskadalur flora, Iceland [ca 65°36′ N, 17°49′W]** 5.5 Ma This study | |
|---|---|
| 2 | Equisetum sp. |
| 1 | Lycopodium |
| 1 | Polypodiaceae gen. et spec. indet. 1 |
| 1 | Polypodiaceae gen et spec. indet. 7 |
| 1 | Polypodiaceae gen. et spec. indet. 8 |
| 1 | Sphagnum sp. |
| 1 | Trilete spore, fam., gen. et spec. indet. 2 |
| 1, 2 | Abies steenstrupiana |
| 1 | Cathaya sp. |
| 1, 3 | Picea sect. Picea |
| 1 | Pinus sp. 1 (Diploxylon type) |
| 1 | Pseudotsuga/Larix sp. |
| 1 | Scyadopitys sp. |
| 1, 3 | Alnus cecropiifolia |
| 1 | Apiaceae gen. et spec. indet. 6 |
| 1 | Apiaceae gen. et spec. indet. 7 |
| 1 | Artemisia sp. 2 |
| 1 | Asteraceae gen. et spec. indet. 1 |
| 1 | Asteraceae gen. et spec. indet. 2 |
| 1 | Asteraceae gen. et spec. indet 4 |
| 1, 3 | Betula cristata |
| 3 | Betula sp. A (section Betulaster) |
| 1 | aff. Calycanthaceae |
| 1 | Caryophyllaceae gen. et spec. indet. 4 |
| 1 | Ericaceae gen. et spec. indet. 2 |
| 1 | Ericaceae gen. et spec. indet. 3 |
| 1 | Liliaceae gen. et spec. indet. 4 |
| 1 | Menyanthes sp. |
| 1 | Myriophyllum sp. 1 |
| 1 | Nuphar sp. |
| 2 | Phragmites sp. |
| 1 | aff. Plantago lanceolata |
| 1 | Poaceae gen. et spec. indet. 2 |
| 3 | Poales fam., gen. et spec. indet. |
| 1 | Pollen type 21 |
| 1 | Pollen type 22 |
| 1 | Pollen type 23 |
| 1 | Polygonum viviparum |
| 1 | Quercus infrageneric group Quercus sp. 2 |
| 1 | Ranunculaceae gen. et spec. indet. 2 |
| 1 | Ranunculaceae gen. et spec. indet. 3 |
| 1 | Ranunculus sp. 1 |
| 1 | Ranunculus sp. 2 |
| 1 | Rosaceae gen. et spec. indet. 10 |

(continued)

| **Fnjóskadalur flora** (continued) | |
|---|---|
| 1 | Rosaceae gen. et spec. indet. 11 |
| 1 | Rosaceae gen. et spec. indet. 12 |
| 1, 3 | Salix gruberi |
| 3 | Salix sp. A |
| 1 | Sanguisorba sp. |
| 1 | Sparganium sp. |
| 1 | Tetracentron atlanticum |
| 1 | Thalictrum sp. 1 |
| 1 | aff. Valeriana sp. |

| **Murat flora, France [45°07′ N, 2°25′ E]** 5.34±0.3 Ma Roiron 1991 | |
|---|---|
| 2 | **Abies ramesi** |
| 3 | Glyptostrobus europaeus |
| 2, 3 | **Picea sp.** |
| 2 | **Pinus sp.** |
| 3 | Sequoia langsdorfii |
| 3 | Acer campestre |
| 3 | Acer integerrimum |
| 2 | Acer opulifolium |
| 2 | Acer platanoides |
| 3 | Acer sanctae-crucis |
| 3 | Acer tricuspidatum |
| 3 | **Alnus glutinosa** |
| 3 | **Alnus hoernesi** |
| 3 | **Alnus sp. cf. A. kefersteinii** |
| 3 | **Alnus viridis** |
| 3 | Bambusa sp. |
| 3 | Berberis sp. cf. B. regeliana |
| 3 | **Betula sp.** |
| 2, 3 | Carpinus betulus |
| 2, 3 | Carpinus suborientalis |
| 3 | Carya minor |
| 3 | Cedrela sp. |
| 3 | Celtis australis |
| 3 | Ceratophyllum demersum |
| 3 | cf. Photinia |
| 3 | Crataegus sp. cf. C. douglasii |
| 3 | Dicotylophyllum sp. 1–5 |
| 3 | Dombeyopsis lobata |
| 3 | Hedera helix |
| 3 | Ilex sp. aff. I. cornuta |
| 3 | Juglans regia |
| 3 | Phellodendron sp. cf. P. amurense |
| 3 | Populus tremula |
| 3 | Prunus acuminata |
| 3 | **Quercus hispanica** |
| 3 | **Quercus kubinyi** |
| 3 | **Quercus sp. cf. Q. macranthera** |
| 3 | Rosa sp. cf. R. californica |
| 3 | Tilia tomentosa |
| 3, 2 | Ulmus campestris |
| 3, 2 | Ulmus sp. cf. U. fulva |
| 3 | Zelkova ungeri aff. Z. acuminata |
| 3 | Zelkova ungeri aff. Z. crenata |

| **Lava Camp flora, Seward Peninsula [65°49′ N, 163°18′ W]** 5.7 ± 0.2 Ma Hopkins et al. 1971 Matthews and Ovenden 1990 | |
|---|---|
| 1 | **Abies** |
| 1 | Cupressaceae/Taxodiaceae (?Chamaecyparis) |
| 1, 2 | **Larix sp. (Larix/Pseudotsuga)** |
| 1, 2 | **Picea glauca** |
| 1, 2 | **Picea mariana** |
| | **Picea sitchensis** |
| 1, 2 | **Pinus monticola** |
| 1, 2 | **Pinus subsect. Cembrae** |
| 1, 2 | **Pinus two-needle type undifferentiated** |
| | Thuja sp. |
| | Tsuga heterophylla |
| 1 | Tsuga mertensiana-type |
| 1 | **Alnus spp.** |
| 1 | **Betula sp.** |
| | Cornus stolonifera |
| 1 | Corylus sp. |
| 1, 2 | Carex spp. |
| 1, 2 | Cyperus spp. |
| | Hippuris sp. |
| | **Menyanthes trifoliata** |
| 1 | Onagraceae |
| | Paliurus sp. |
| 1 | **Poaceae** |
| 1 | **Salix sp.** |
| 1, 2 | Symphoricarpos sp. |
| 1, 2 | Vaccinium sp. |

Boldface indicates that the genus is present in the 5.5 formation. Grey shading indicates that the genus is present in the younger Tjörnes beds and/or the older Hreðavatn-Stafholt Formation. *1* based on pollen, spores; *2* based on leaves and/or fruit/seed fossils; *3* based on leaf fossils.

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## Explanation of Plates

**Plate 9.1** **1**. Selárgil in Fnjóskadalur, Fnjóskadalur Formation (ca 5.5 Ma). View up the gully Selárgil, outcrop seen in the distance to the left. **2**. View over the upper part of the Selárgil gully, outcrop below the massive columnar basalt. **3**. Selárgil outcrop, geologist digging for fossils. **4**. Upper part of the sedimentary section, showing the brown sandy siltstones. **5**. Contact zone between basalt and sediments. **6**. Detail showing fine grained clay-rich siltstones and the white tephra layer at the bottom were the pollen originate from. **7–10**. Preservation of fossils, compressions and impressions in siltstone (**7, 9**), and fine grained sandstone (**8**), and a lignified part of stem. Reddish colour caused due to oxidization by weathering

**Plate 9.2** **1–3**. *Sphagnum* sp. **1**. Spore in SEM, distal polar view. **2**. Detail of spore surface. **3**. Spore in LM, proximal polar view showing trilete tetrad mark. **4–6**. *Sphagnum* sp. **4**. Spore in SEM, proximal polar view. **5**. Detail of spore surface. **6**. Spore in LM, proximal polar view

showing trilete tetrad mark. **7**–**9**. *Lycopodium* sp. **7**. Spore in SEM, distal polar view. **8**. Detail of spore surface. **9**. Spore in LM, oblique polar view. **10**–**12**. *Lycopodium* sp. **10**. Spore in SEM, proximal polar view showing trilete tetrad mark. **11**. Detail of spore surface. **12**. Spore in LM, polar view

**Plate 9.3** **1**–**3**. Polypodiaceae gen. et spec. indet. 1. **1**. Spore in SEM, equatorial view showing monolete tetrad mark. **2**. Detail of spore surface. **3**. Spore in LM, equatorial view. **4**–**6**. Polypodiaceae gen. et spec. indet. 7. **4**. Spore in SEM, equatorial view. **5**. Detail of spore surface. **6**. Spore in LM, equatorial view. **7**–**9**. Polypodiaceae gen. et spec. indet. 8. **7**. Spore in SEM, oblique equatorial view. **8**. Detail of spore surface. **9**. Spore in LM, oblique equatorial view. **10**–**12**. Trilete spore fam. gen. et spec. indet. 2. **10**. Spore in SEM, distal polar view. **11**. Detail of spore surface. **12**. Spore in LM, proximal polar view showing trilete tetrad mark

**Plate 9.4** **1**. *Equisetum* sp., underground rhizome (IMNH org 65-02). **2**. *Equisetum* sp., detail showing part of aerial stem (IMNH org 67). **3**. *Equisetum* sp., part of stem (IMNH 4326-03). **4**. *Equisetum* sp., detail showing sheath (IMNH org 67). **5**. *Abies steenstrupiana*, cone scale (IMNH org 65-01). **6**. *Picea* sect. *Picea*, needle (IMNH org 62-02). **7**. Poales fam. gen. et spec. indet. 2. (IMNH 6823). **8**. *Phragmites* sp., part of stem (IMNH 4325-02)

**Plate 9.5** **1**–**3**. *Abies* sp. **1**. Bisaccate pollen grain in SEM, proximal polar view. **2**. Detail of corpus surface. **3**. Bisaccate pollen grain in LM, polar view. **4**. *Pinus* sp. 1 (Diploxylon type), bisaccate pollen grain, equatorial view. **5**. *Cathaya* sp., bisaccate pollen grain, polar view. **6**–**8**. *Larix/Pseudotsuga* sp. **6**. Pollen grain in SEM. **7**. Detail of pollen grain surface. **8**. Pollen grain in LM. **9**–**11**. *Sciadopitys* sp. **9**. Pollen grain in SEM, distal polar view. **10**. Detail of pollen grain surface. **11**. Pollen grain in LM

**Plate 9.6** **1**–**3**. Apiaceae gen. et spec. indet. 6. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4**–**6**. Apiaceae gen. et spec. indet. 7. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7**–**10**. *Artemisia* sp. 2. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, polar view (upper), equatorial view (lower). **10**–**12**. *Artemisia* sp. 2. **10**. Pollen grain in SEM, oblique view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, polar view

**Plate 9.7** **1**–**3**. Asteraceae gen. et spec. indet. 1 (Liguliflorae) **1**. Pollen grain in SEM. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM. **4**–**6**. Asteraceae gen. et spec. indet. 2. **4**. Pollen grain in SEM, polar view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, polar view. **7**–**9**. Asteraceae gen. et spec. indet 4. **7**. Pollen grain in SEM. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM

**Plate 9.8** **1**. *Alnus cecropiifolia*, large wide ovate leaf (IMNH 4333) **2**. *Betula cristata*, lower part of leaf, cordate base (IMNH 4332)

**Plate 9.9** **1**. *Betula* sp. A (section *Betulaster*) (IMNH 4339-02). **2**. Detail of Fig. 1 showing teeth along margin

**Plate 9.10** **1**–**3**. *Alnus* sp. 1. **1**. Pollen grain in SEM, polar view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, polar view. **4**–**6**. *Betula* sp. **4**. Pollen grain in SEM oblique equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, polar view. **7**–**9**. *Betula* sp. **7**. Pollen grain in SEM, polar view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, polar view. **10**. *Betula* sp., pollen grain in LM, polar view. **11**. *Betula* sp., pollen grain in LM, polar view

**Plate 9.11** **1–3**. aff. Calycanthaceae sp. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4–6**. Caryophyllaceae gen. et spec. indet. 4. **4**. Pollen grain in SEM. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM. **7–9**. Ericaceae gen. et spec. indet. 2. **7**. Tetrad in SEM. **8**. Detail of tetrad surface. **9**. Tetrad in LM

**Plate 9.12** **1–3**. Ericaceae gen. et spec. indet. 3. **1**. Tetrad in SEM. **2**. Detail of tetrad surface. **3**. Tetrad in LM. **4–6**. *Quercus* infrageneric group *Quercus* sp. 2. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7–9**. *Quercus* infrageneric group *Quercus* sp. 2. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view. **10–12**. *Myriophyllum* sp. 1. **10**. Pollen grain in SEM, oblique polar view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, polar view

**Plate 9.13** **1–3**. Liliaceae gen. et spec. indet. 4. **1**. Pollen grain in SEM. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM. **4–6**. *Menyanthes* sp. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7–9**. *Nuphar* sp. **7**. Pollen grain in SEM. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM. **10–12**. *Plantago lanceolata*. **10**. Pollen grain in SEM. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM

**Plate 9.14** **1–3**. Poaceae gen. et spec. indet. 2. **1**. Pollen in SEM. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM. **4–6**. *Polygonum viviparum*. **4**. Pollen grain SEM, equatorial view. **5**. Detail of pollen grain surface, polar area. **6**. Pollen grain in LM, equatorial view. **7–9**. *Ranunculus* sp. 1. **7**. Pollen grain in SEM. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM. **10–12**. *Ranunculus* sp. 2. **10**. Pollen grain in SEM, equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, equatorial view

**Plate 9.15** **1–3**. *Thalictrum* sp. 1. **1**. Pollen grain in SEM. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM. **4–6**. Ranunculaceae gen. et spec. indet 2. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7–9**. Ranunculaceae gen. et spec. indet 2. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen in LM, equatorial view. **10–12**. Ranunculaceae gen et spec. indet 3. **10**. Pollen grain in SEM, equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, equatorial view

**Plate 9.16** **1–3**. *Sanguisorba* sp. **1**. Pollen grain in SEM, polar view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, polar view. **4–6**. *Sanguisorba* sp. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7–9**. Rosaceae gen. et spec. indet. 10. **7**. Pollen in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view. **10–12**. Rosaceae gen. et spec. indet. 10. **10**. Pollen grain in SEM, equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, equatorial view

**Plate 9.17** **1–3**. Rosaceae gen. et spec. indet. 11. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4–6**. Rosaceae gen. et spec. indet. 12. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7–9**. *Salix* sp. 4. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view. **10–12**. *Salix* sp. 5. **10**. Pollen grain in SEM, equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, equatorial view

**Plate 9.18** **1**. *Salix gruberi*, lower part of large leaf (IMNH org 63-01). **2**. Detail of Fig. 1 showing venation and teeth along margin. **3**. *Salix* sp. A, narrow elliptic leaf (IMNH 4326-01). **4**. Detail of Fig. 3 showing venation along margin. **5**. *Salix gruberi*, upper half of leaf (IMNH 4325-01). **6**. *Salix gruberi*, lower part of leaf (IMNH 4324)

**Plate 9.19** **1**–**3**. *Sparganium* sp. **1**. Pollen grain in SEM. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM. **4**–**6**. *Tetracentron atlanticum*. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **7**–**9**. aff. *Valeriana* sp. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen in LM, polar view

**Plate 9.20** **1**–**3**. Pollen type 21. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, polar view (left), equatorial view (right). **4**–**6**. Pollen type 22. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7**–**9**. Pollen type 23. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view

# Plates




**Plate 9.1**

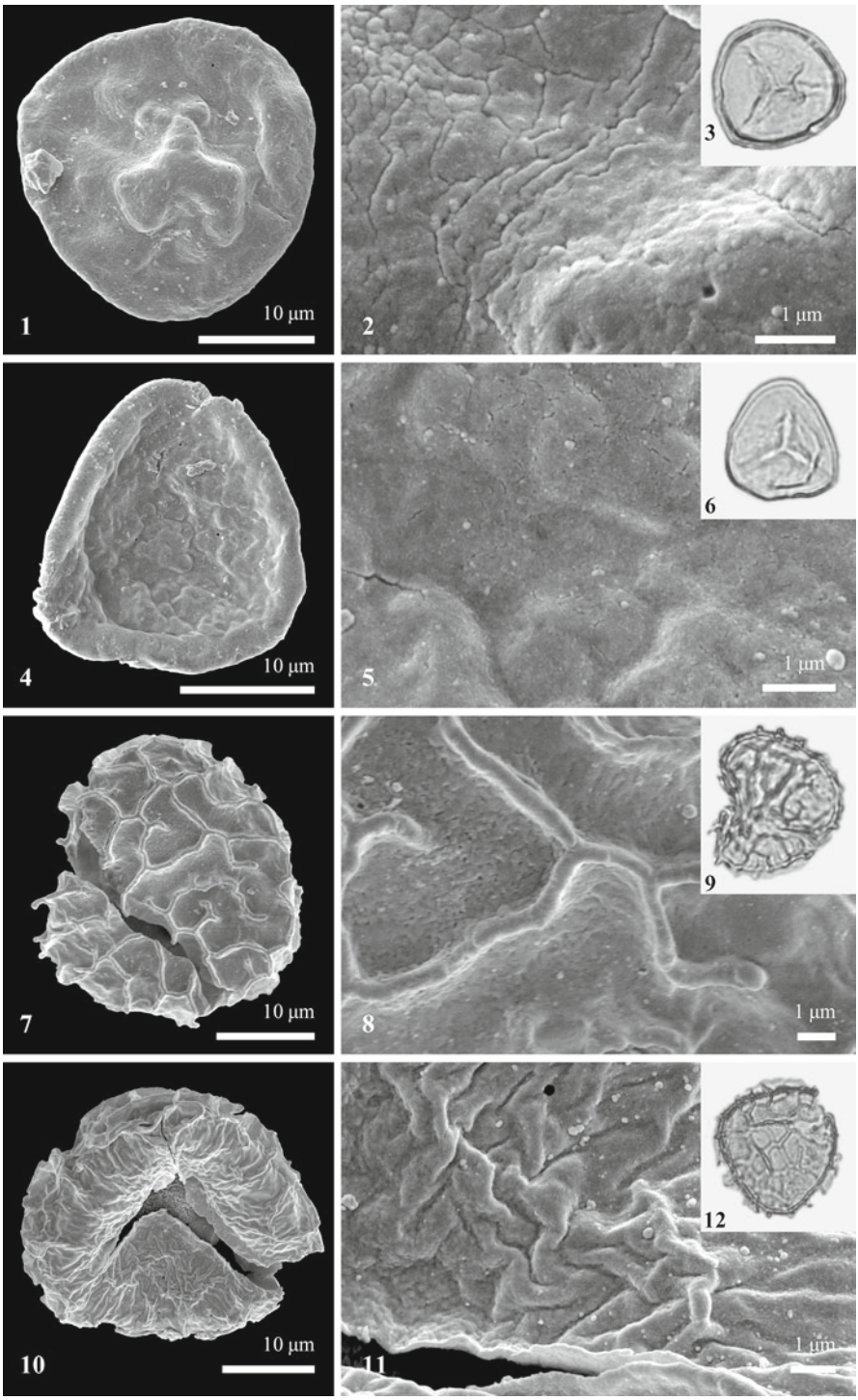



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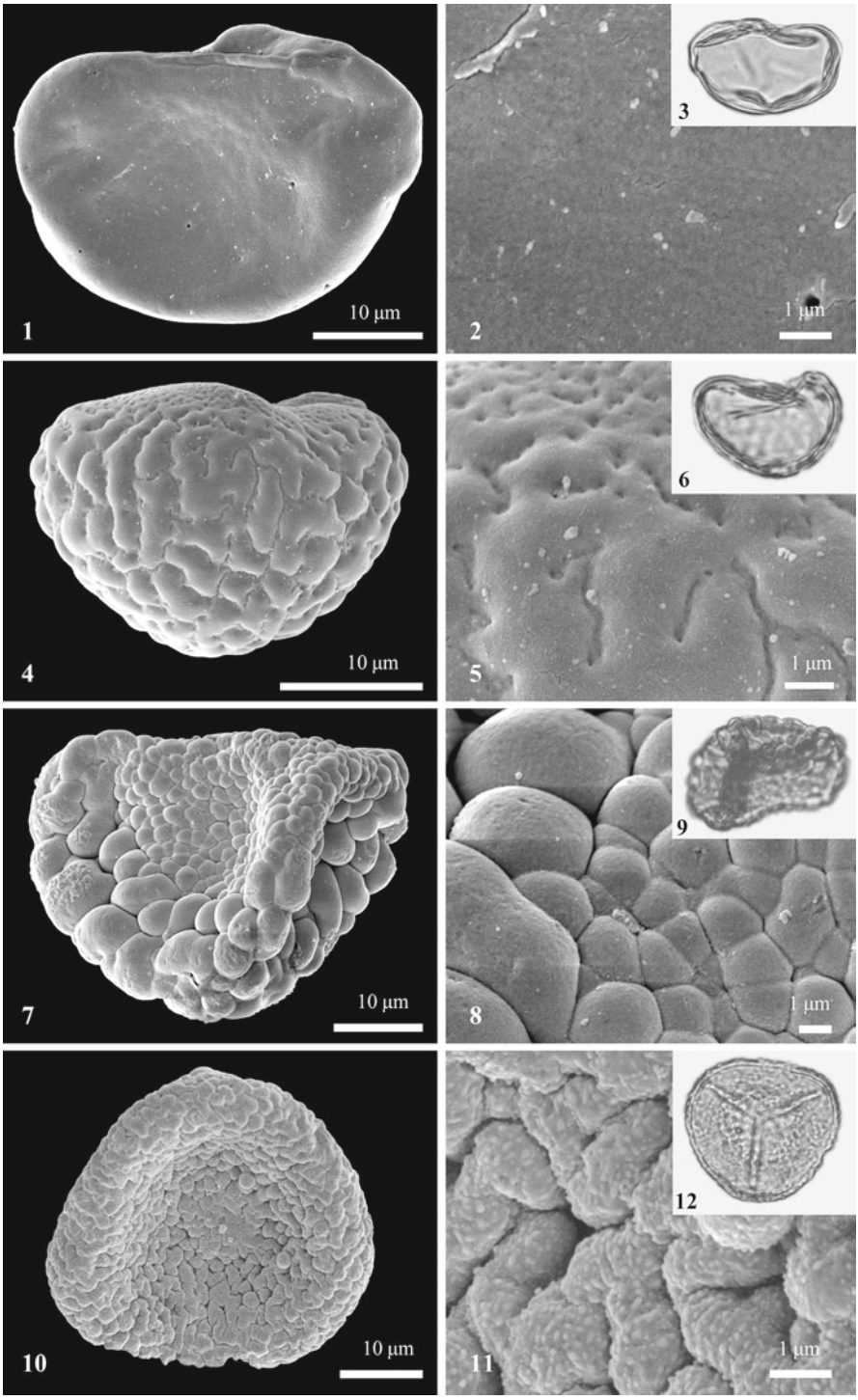



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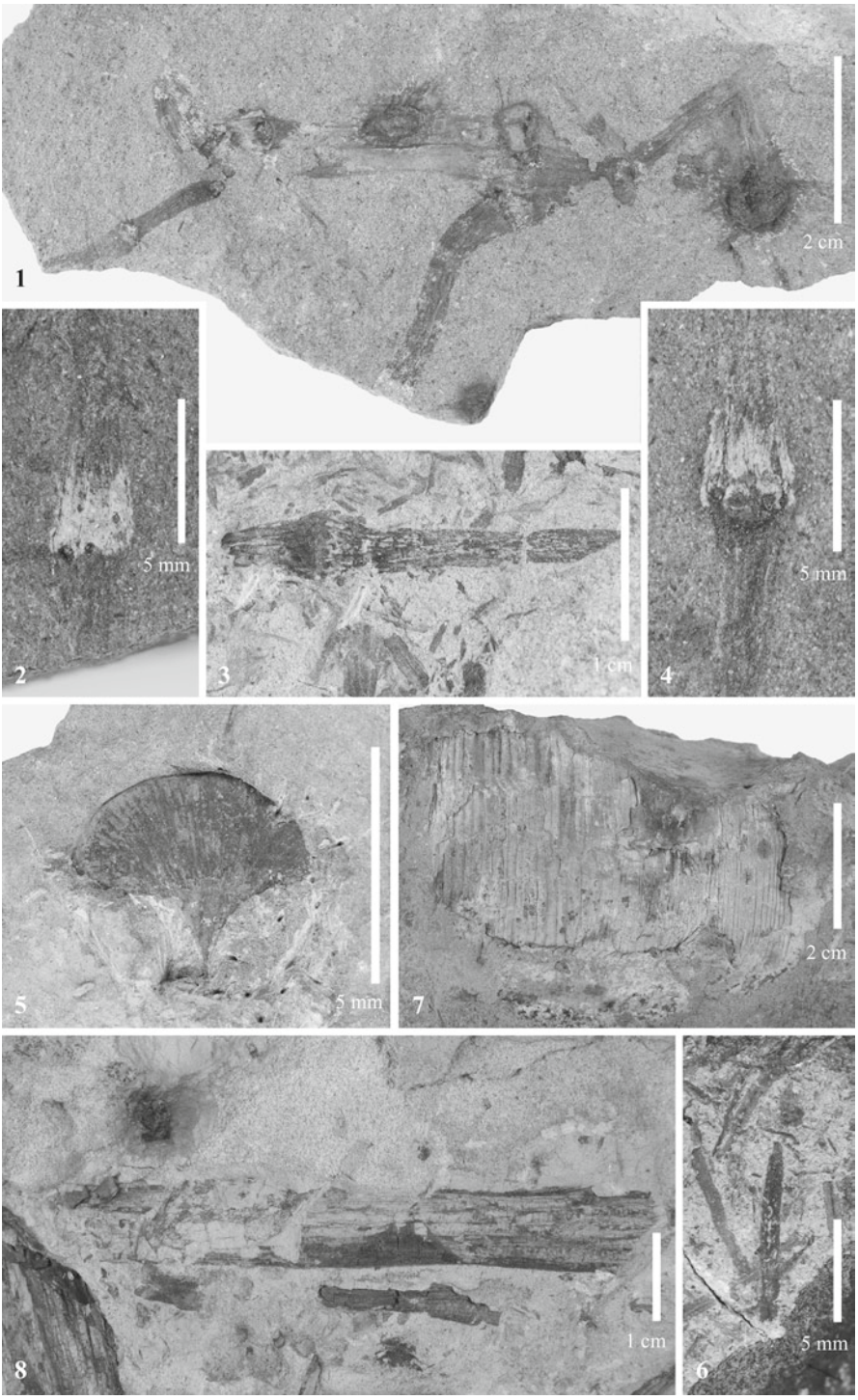



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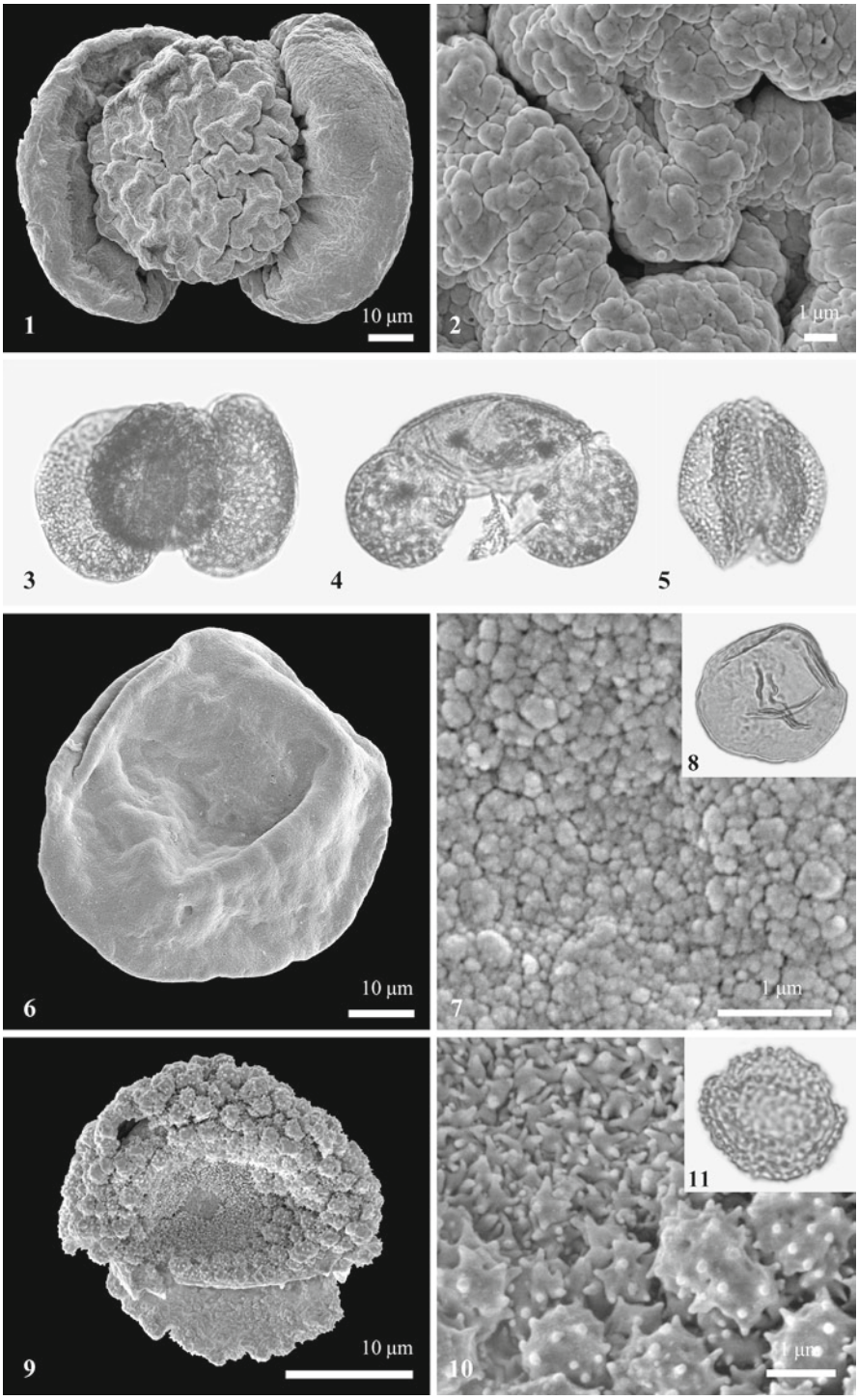



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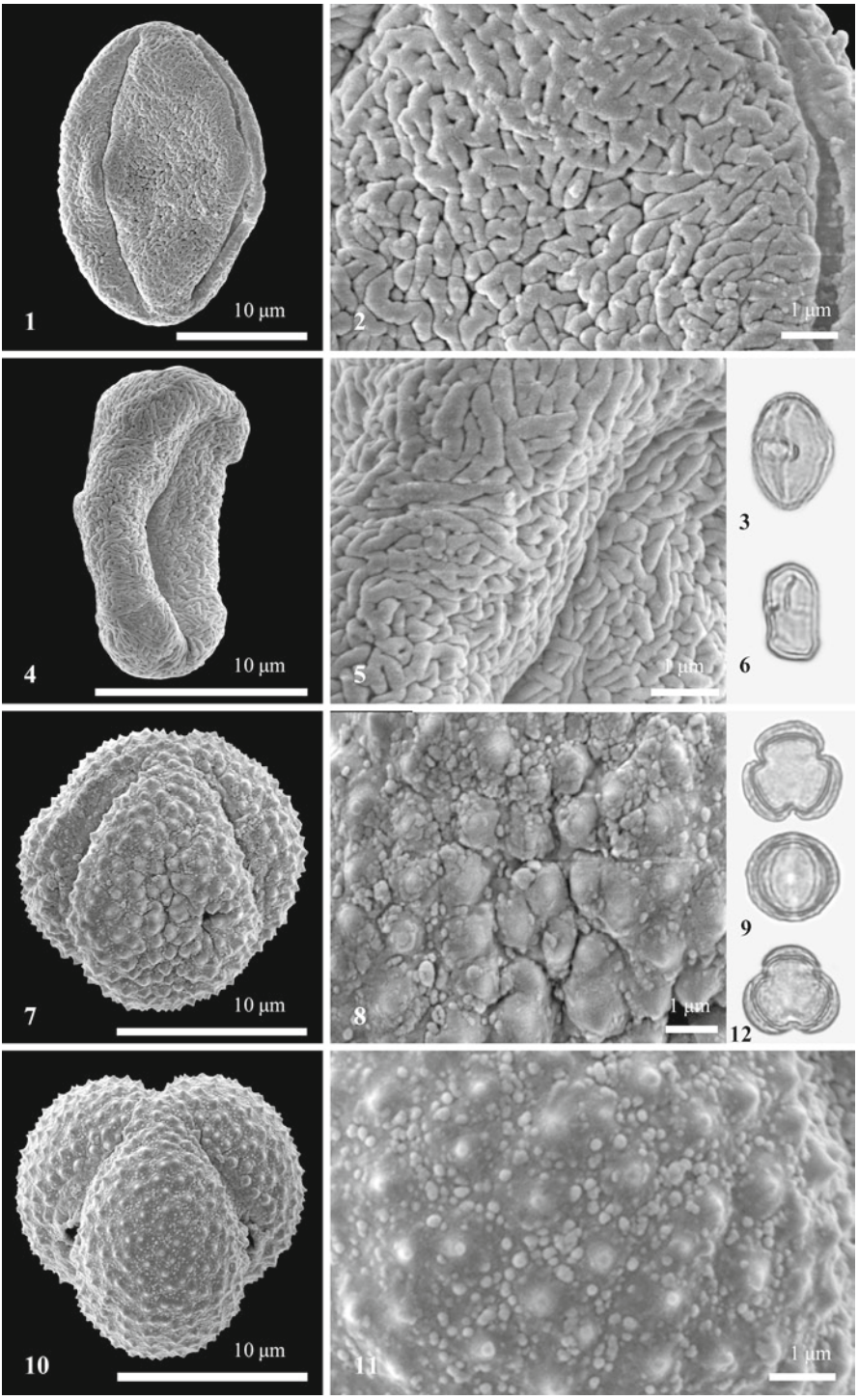



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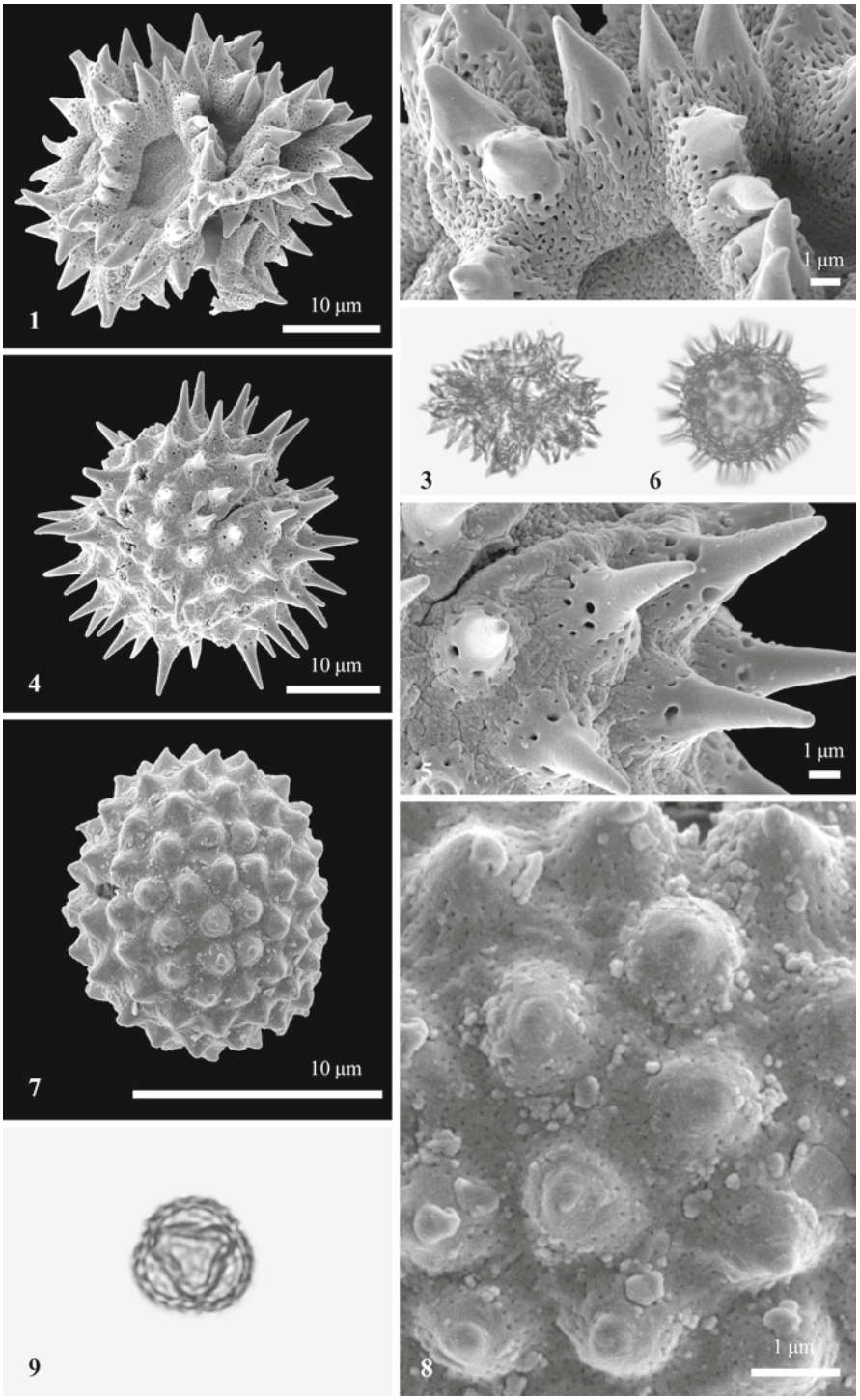



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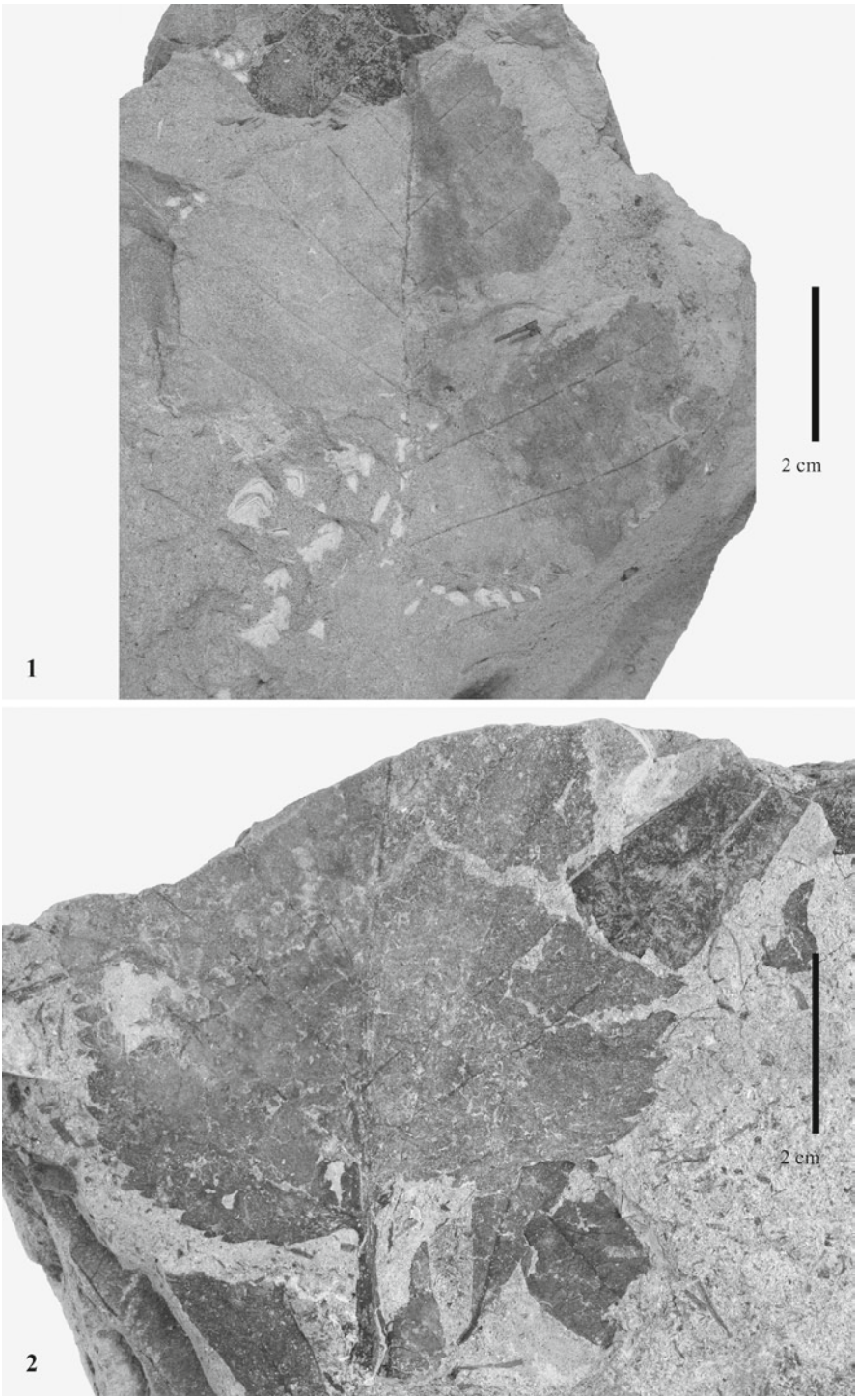



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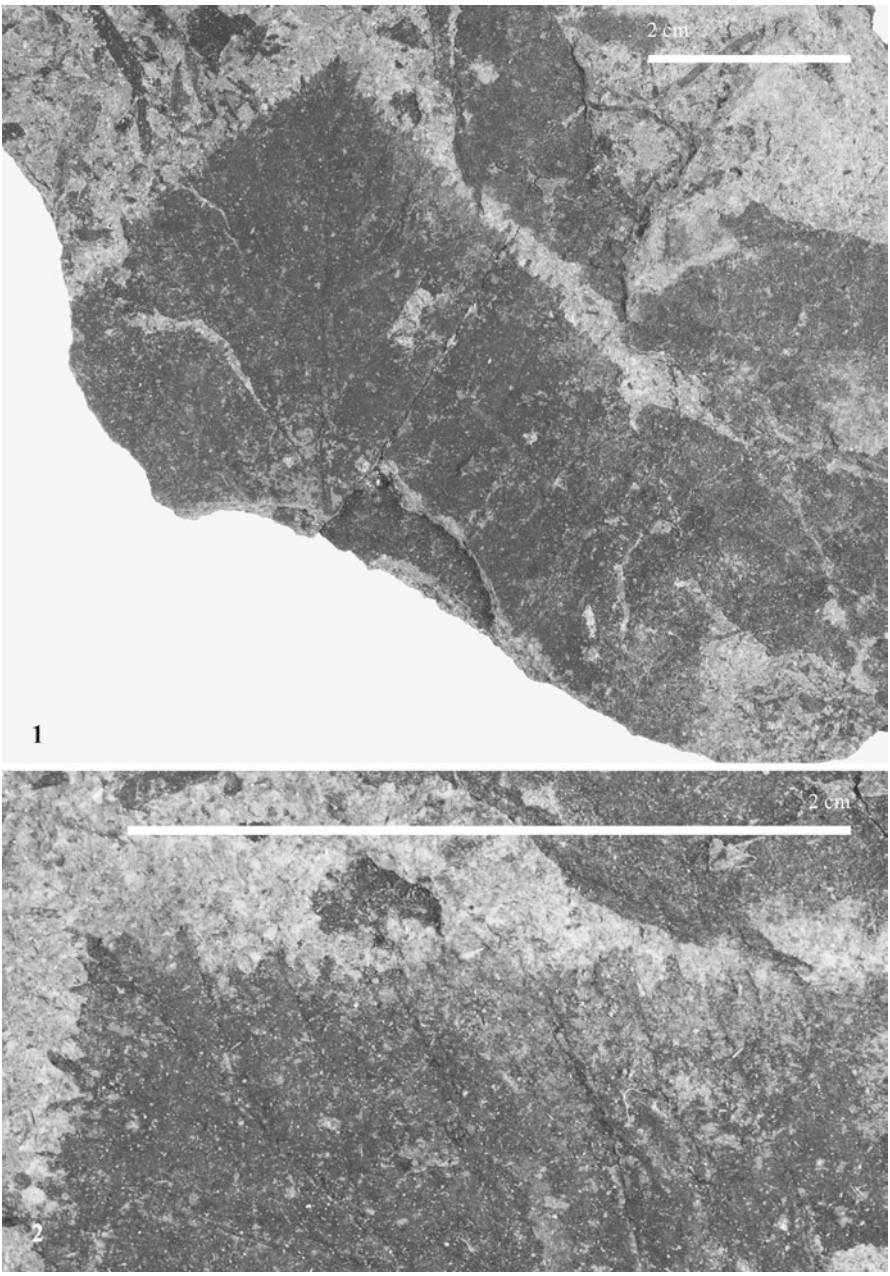



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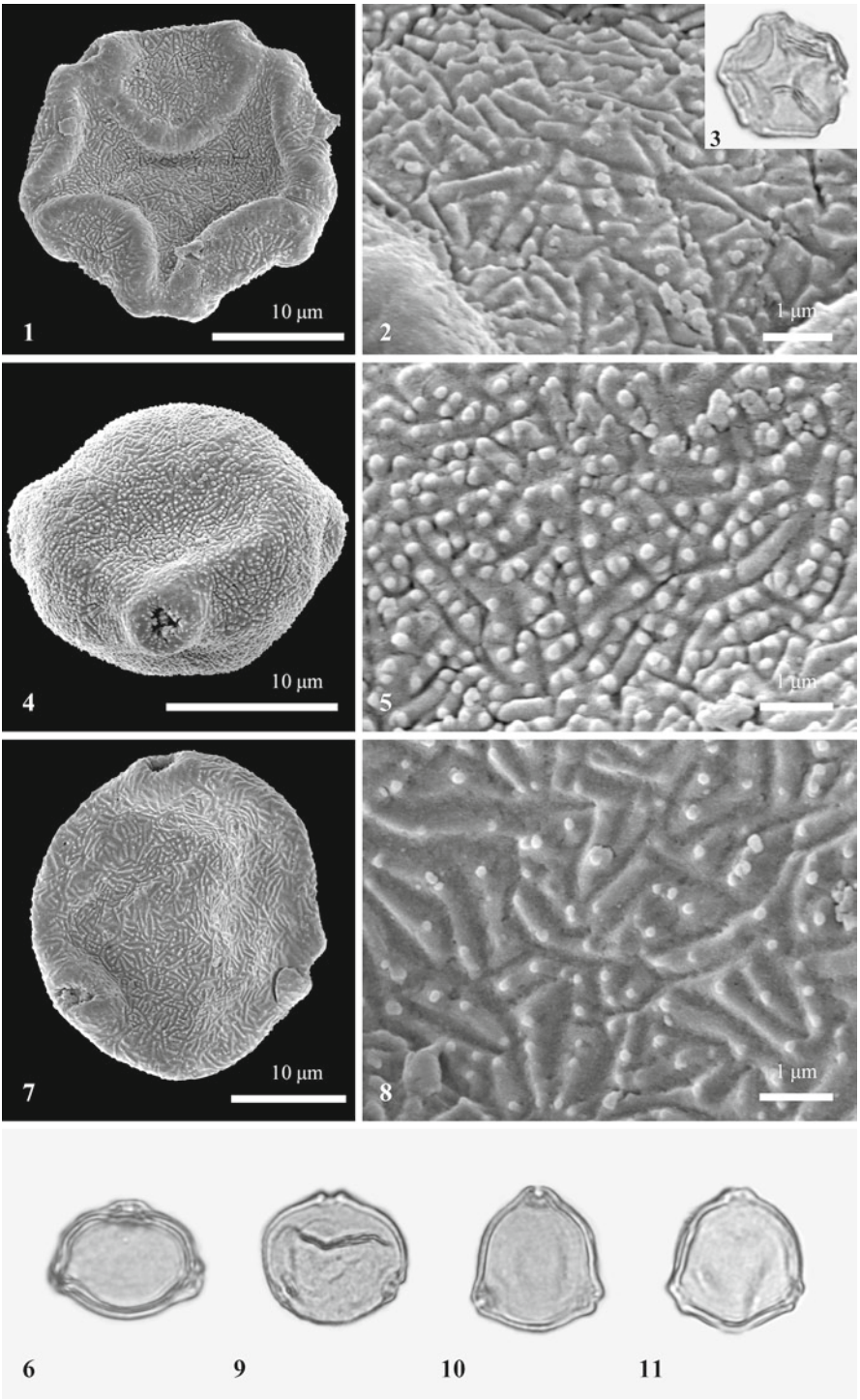



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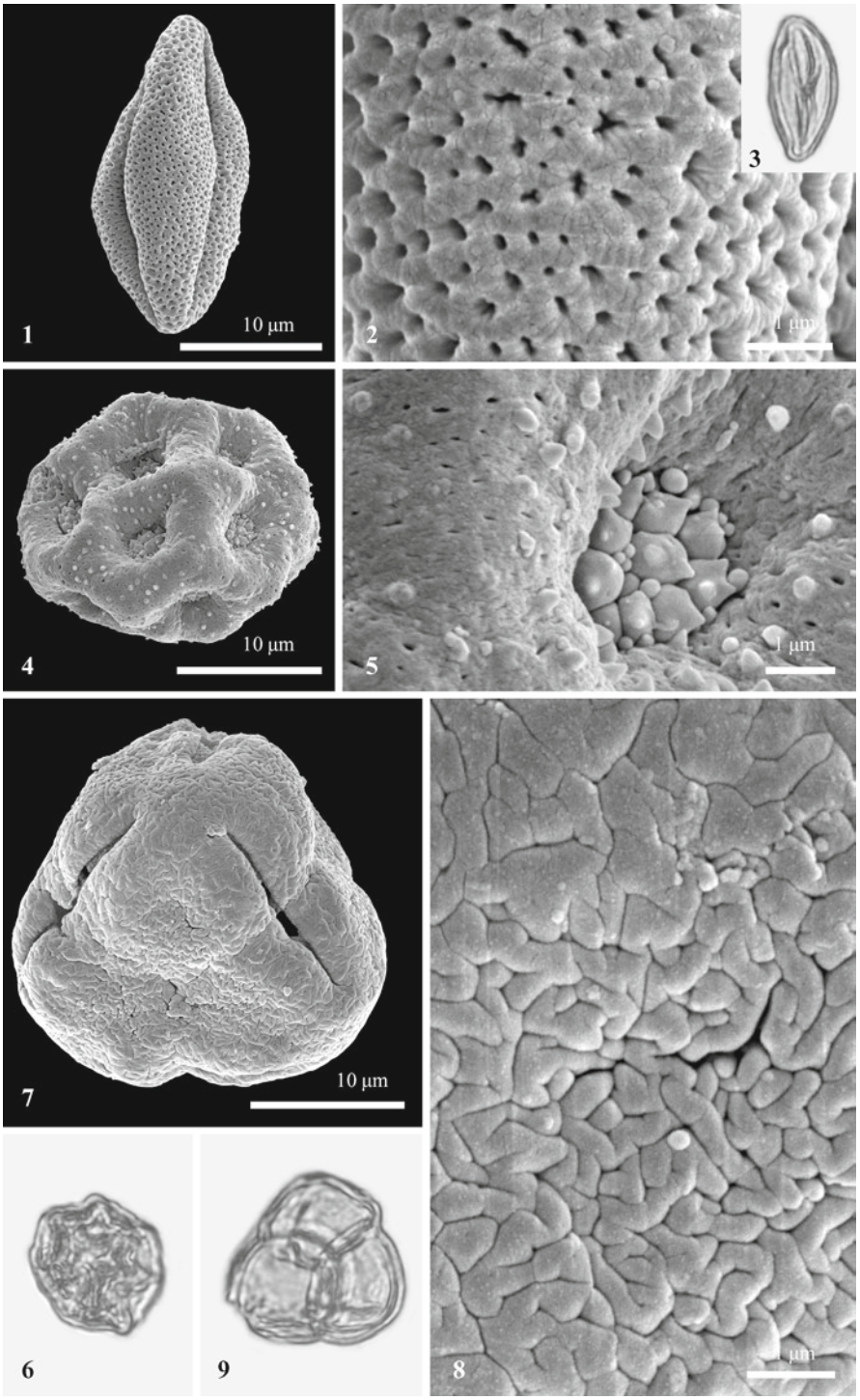



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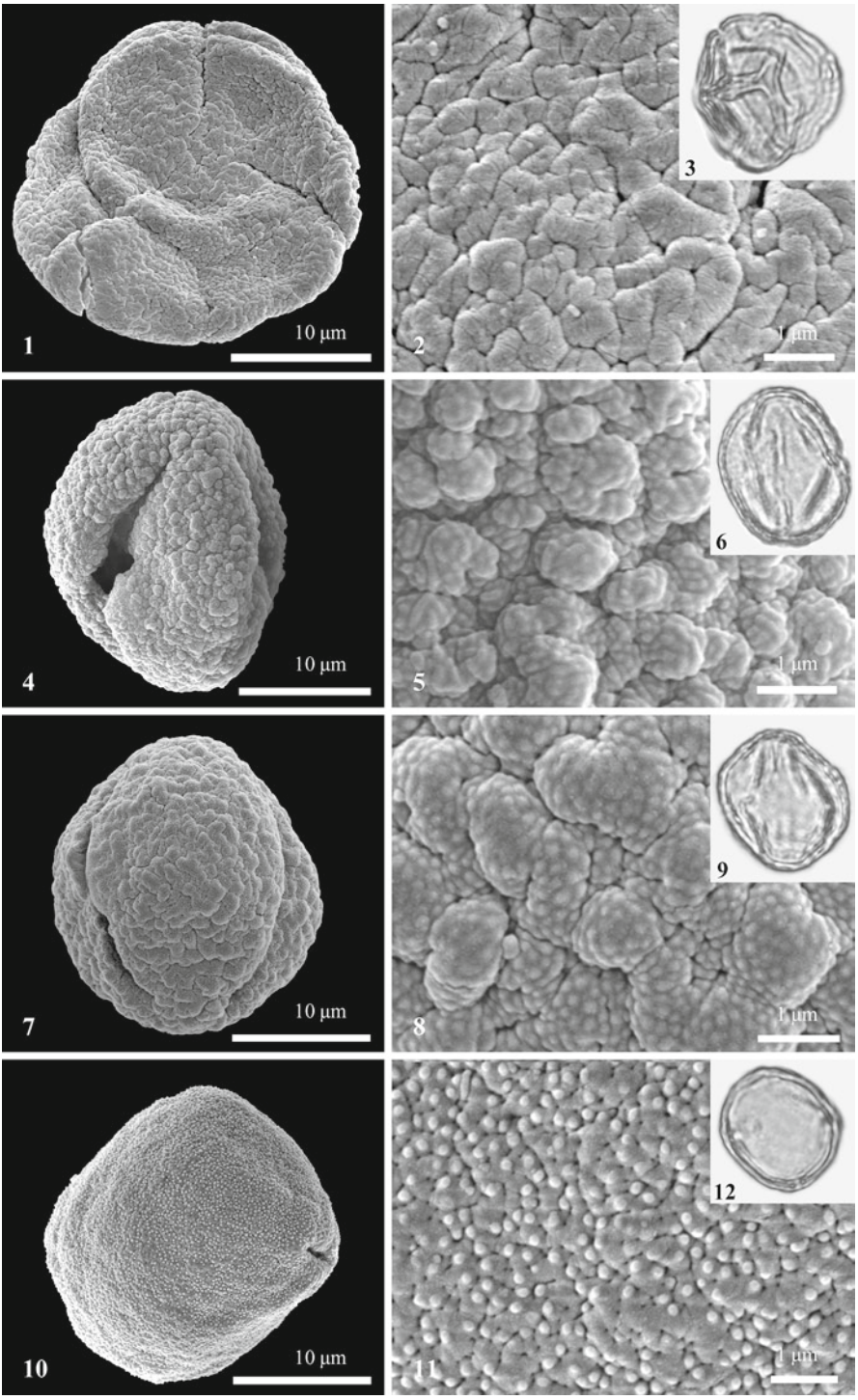



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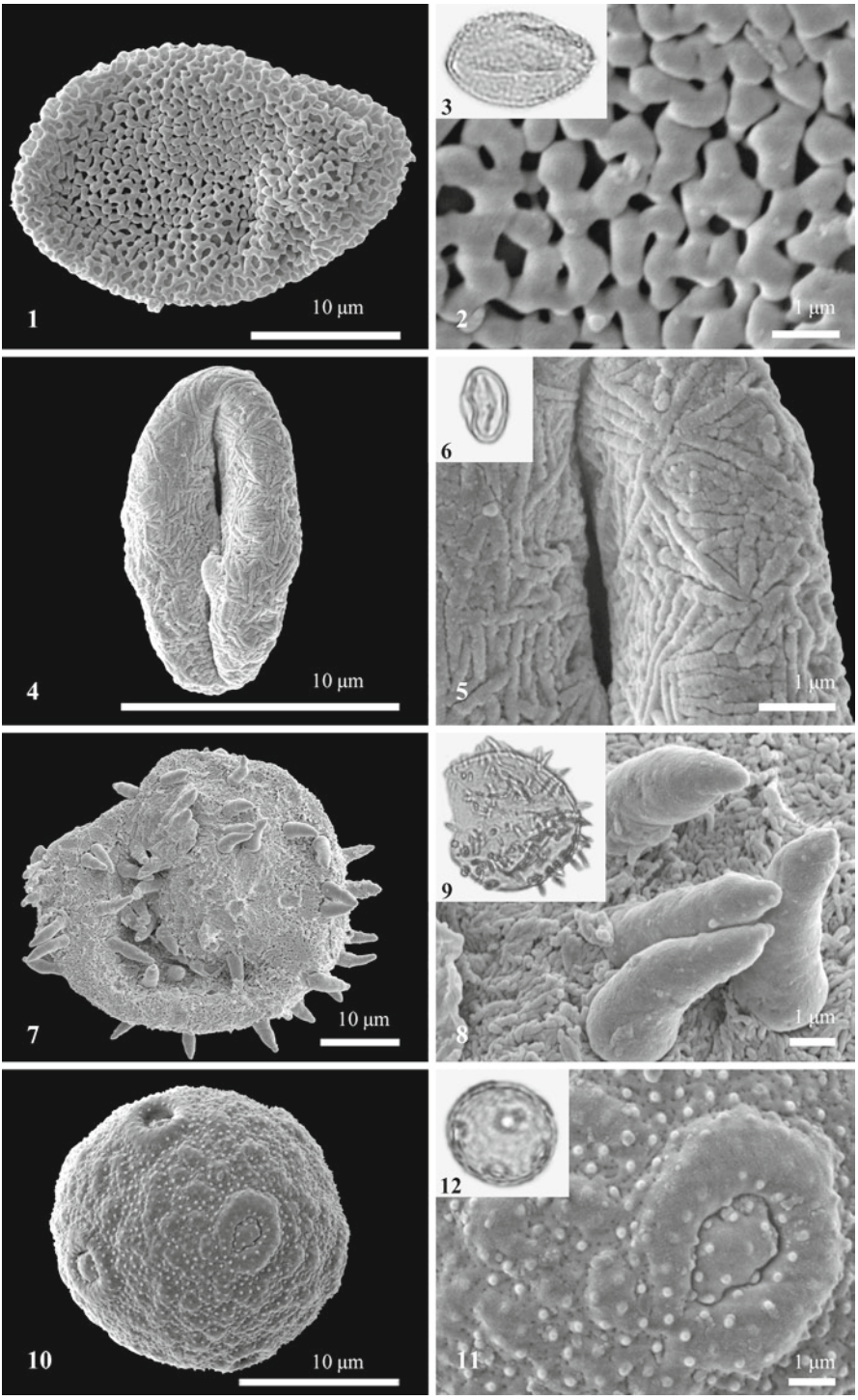



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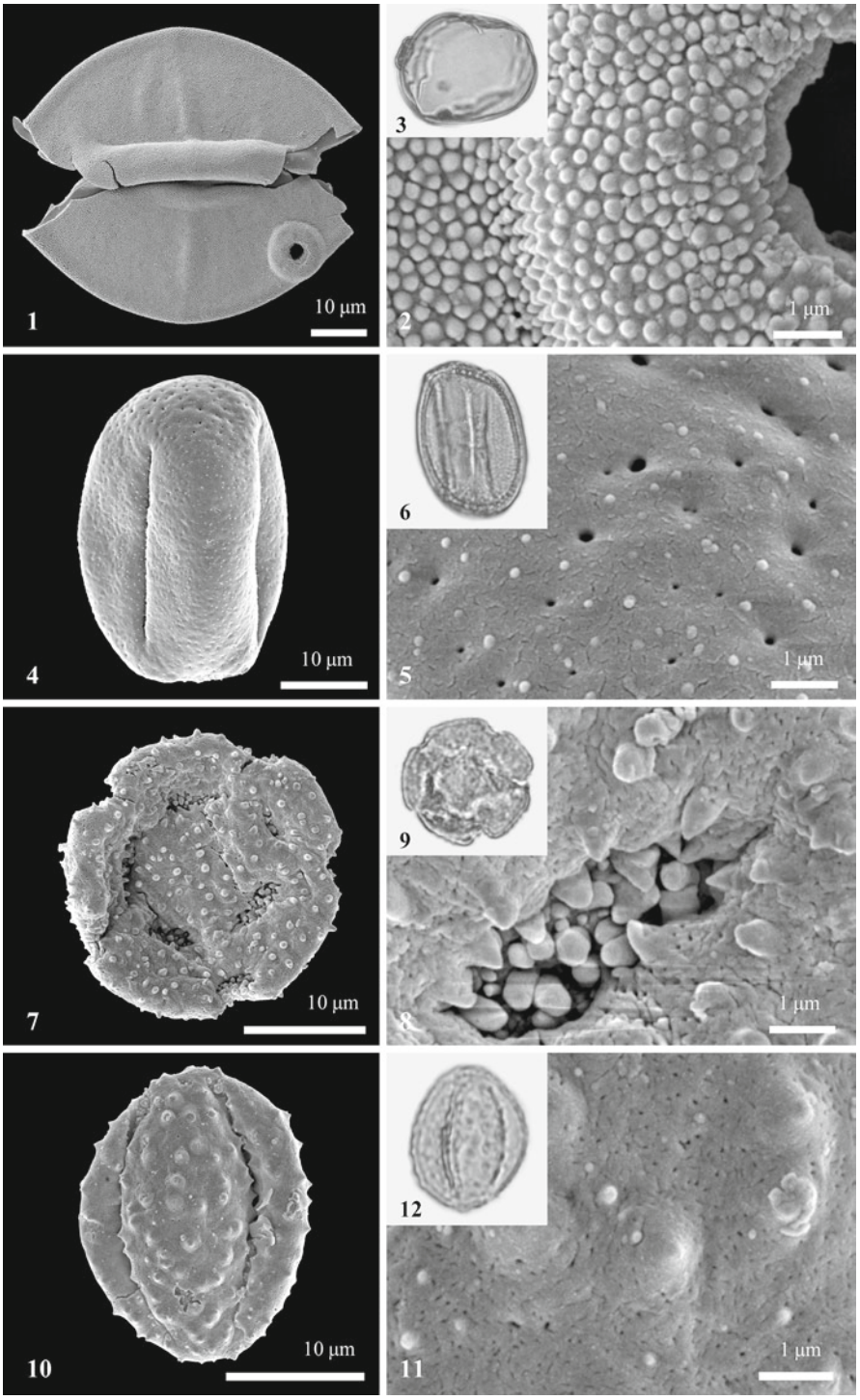



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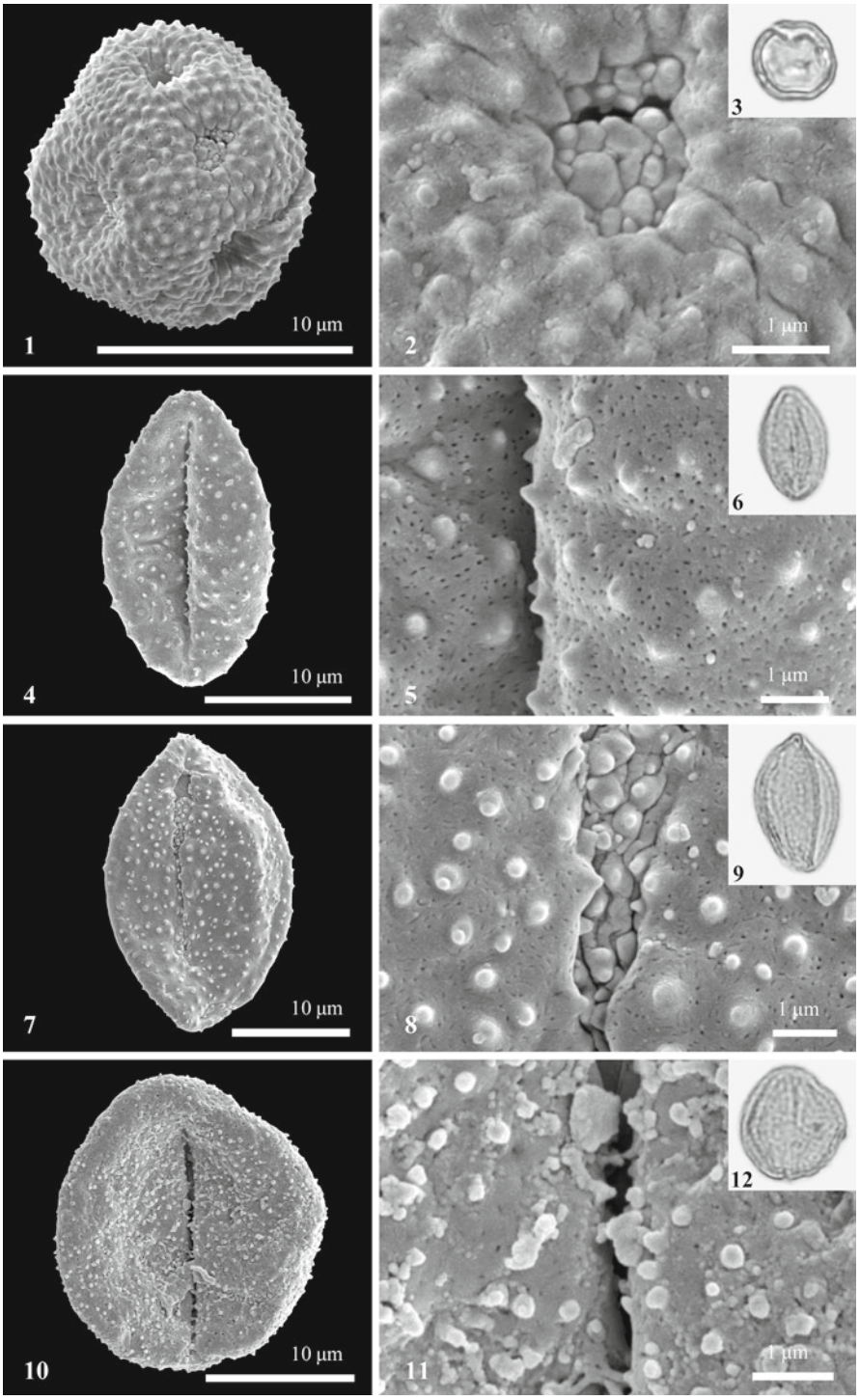



**Plate 9.15**

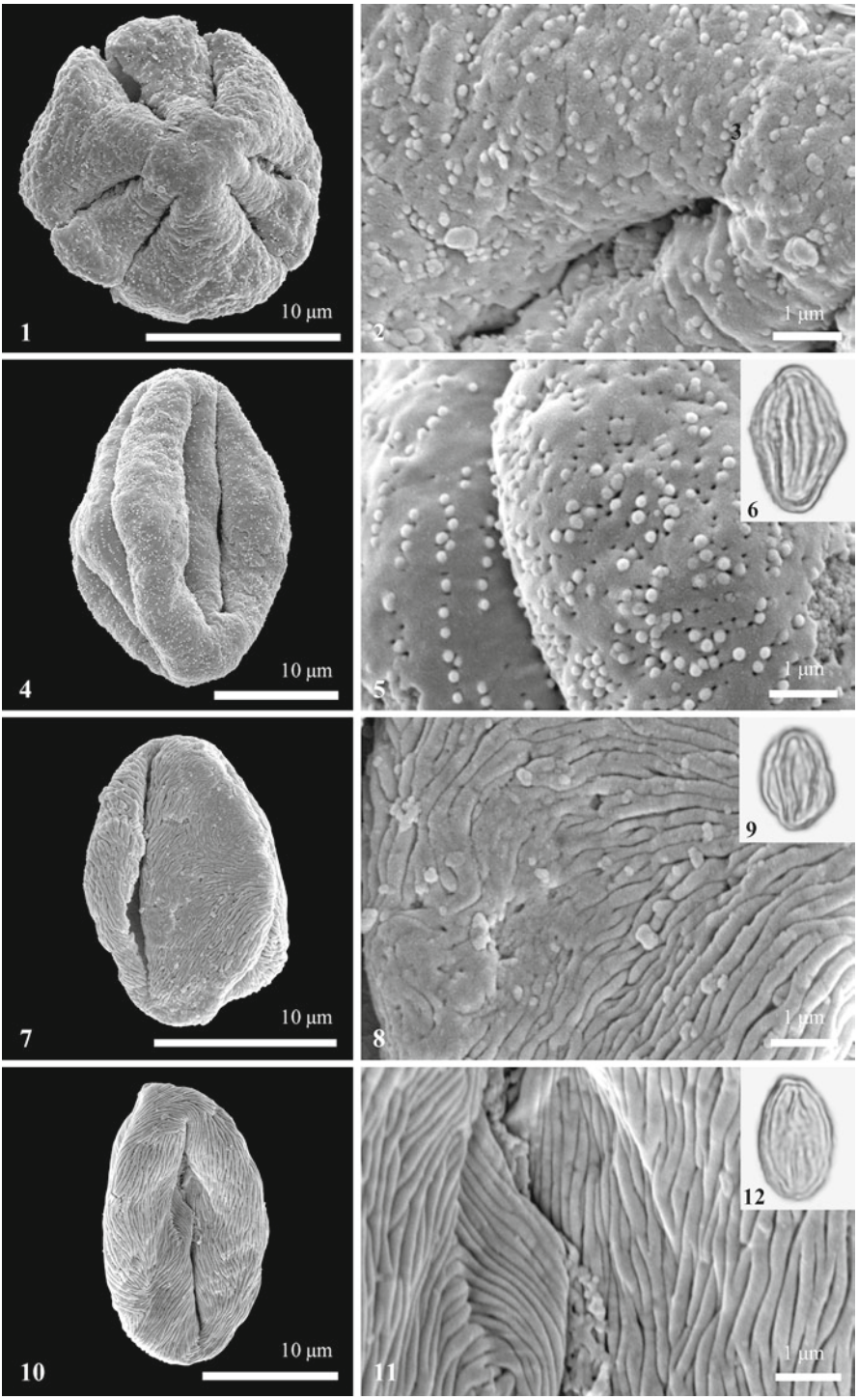



**Plate 9.16**

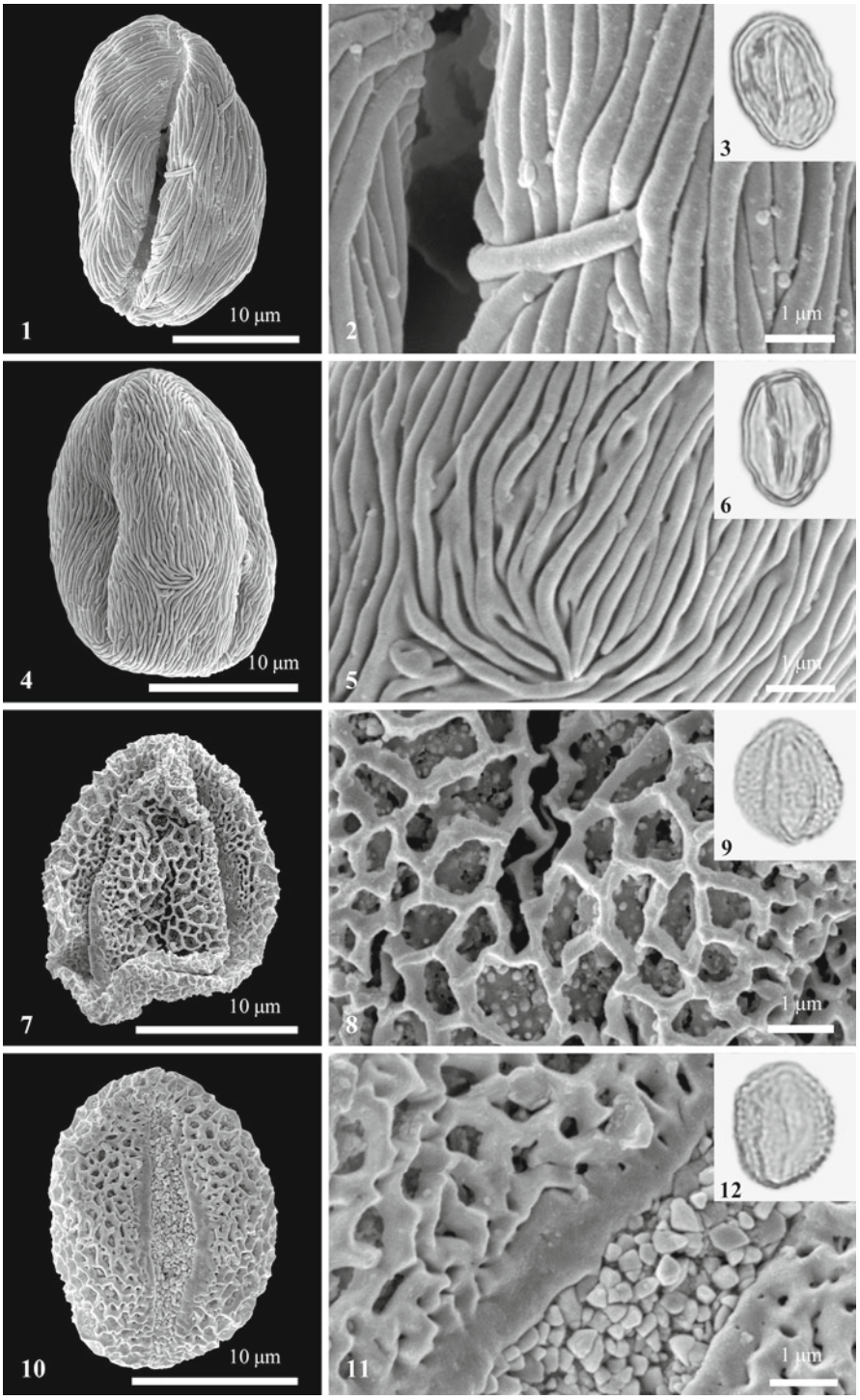



**Plate 9.17**

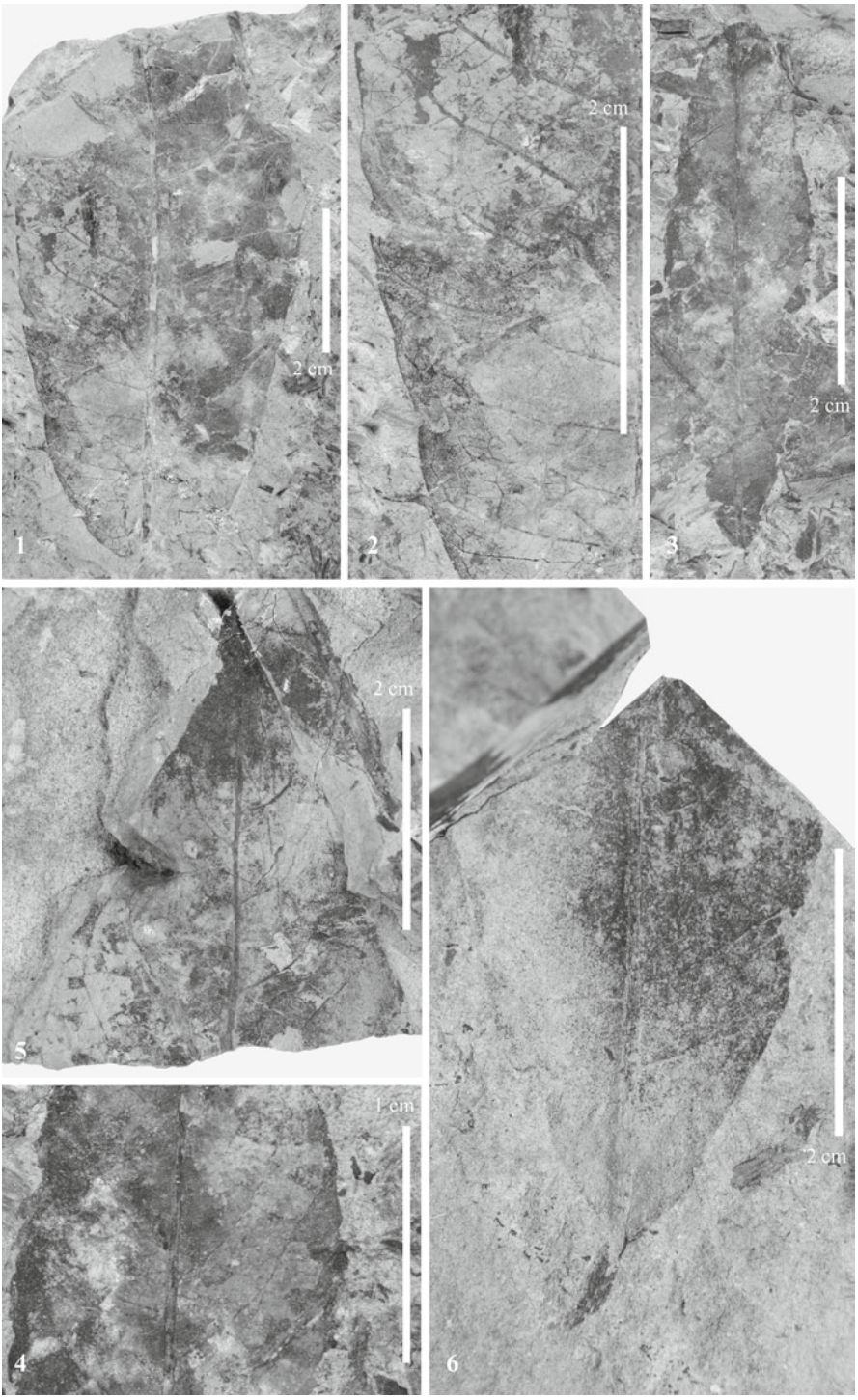



**Plate 9.18**

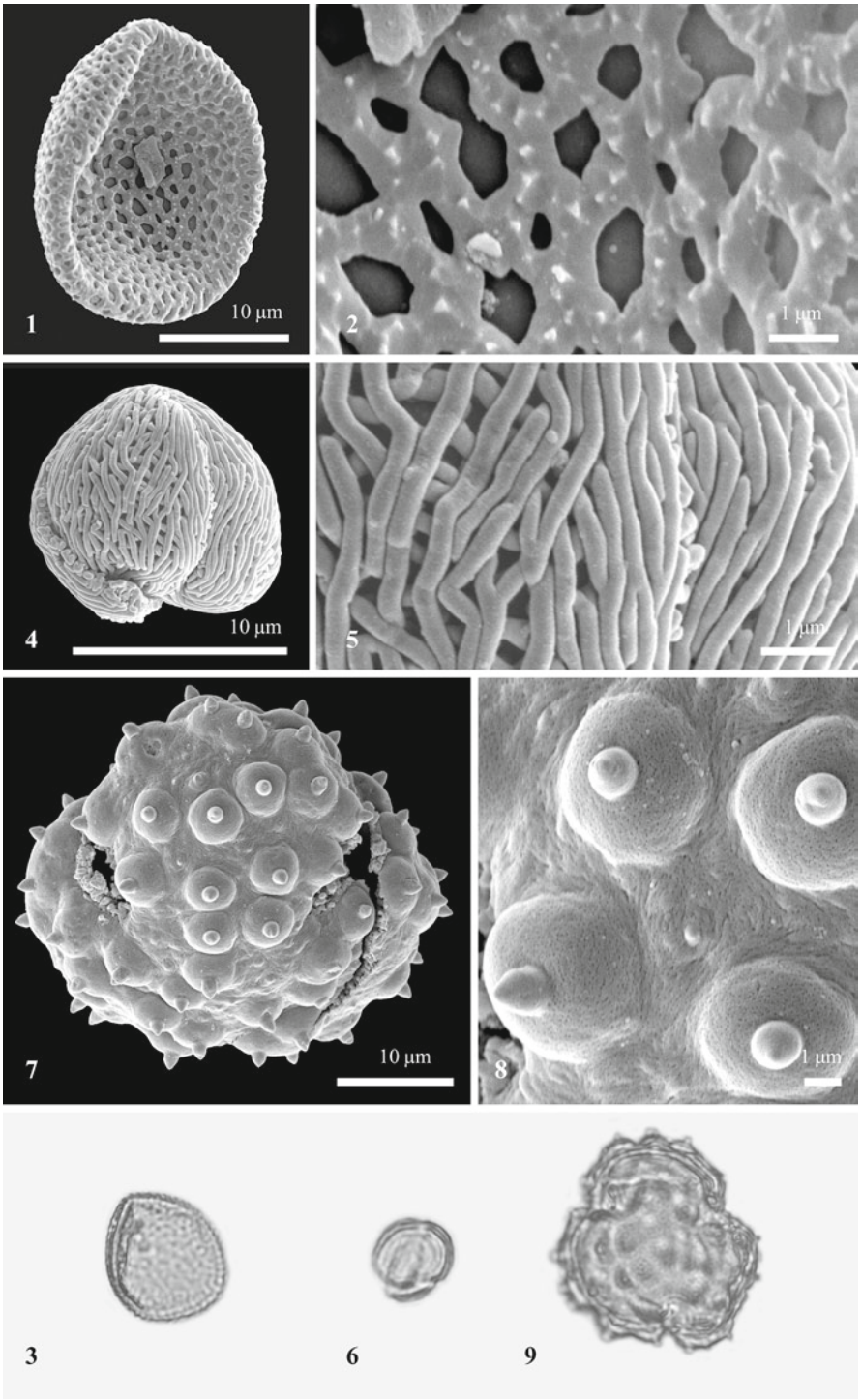



**Plate 9.19**

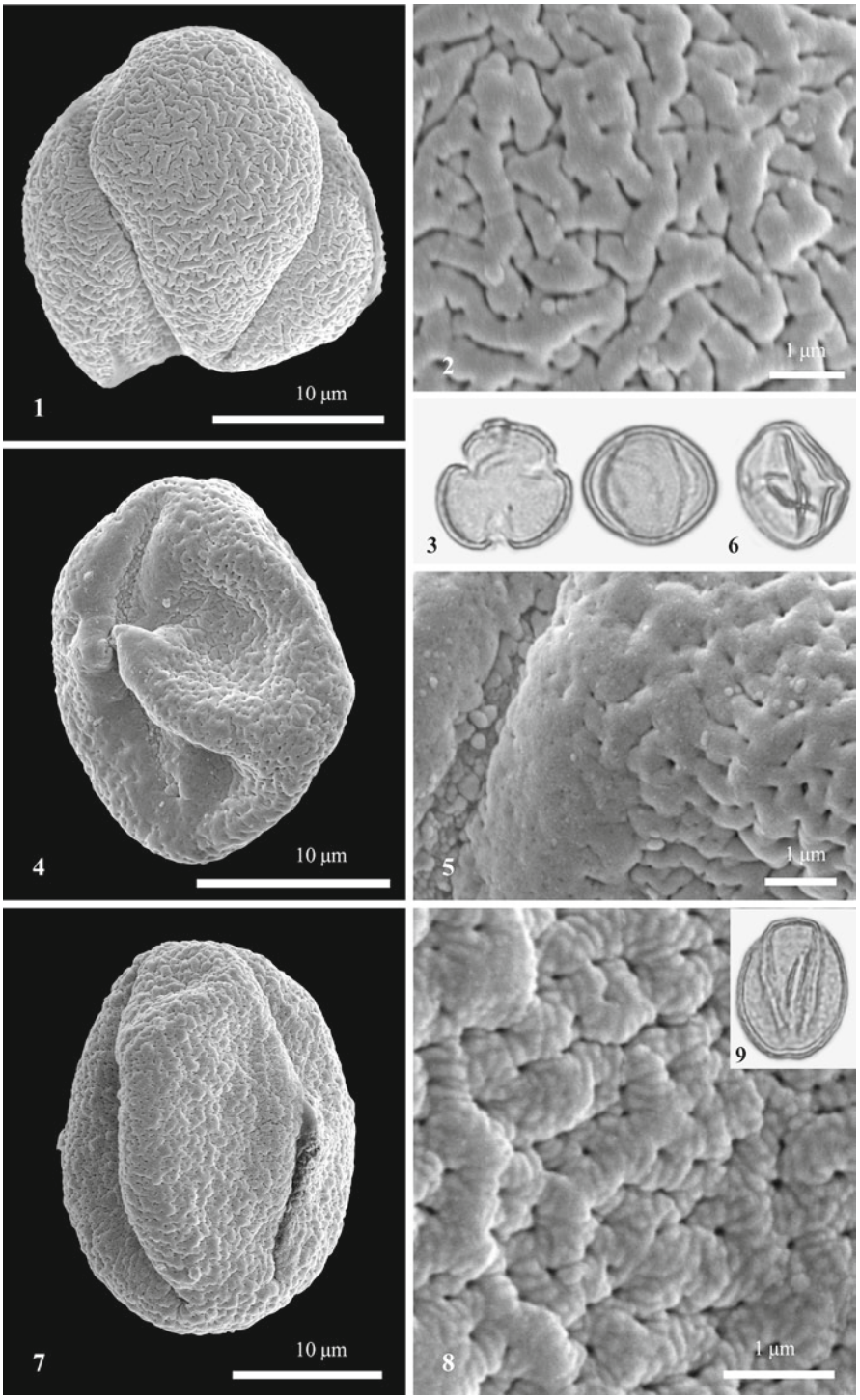



**Plate 9.20**

# Chapter 10
# Pliocene Terrestrial and Marine Biota of the Tjörnes Peninsula: Warm Climates and Biogeographic Re-arrangements

**Abstract** A thick sequence of fossiliferous sediments on the Tjörnes Peninsula in northern Iceland records the vegetation, faunal and climatic histories of the northern North Atlantic region during the Mid-Pliocene Climatic Optimum. The Tjörnes beds are divided into three biozones, the *Tapes* Zone (ca 4.4–4 Ma), the *Mactra* Zone (4–3.6 Ma), and the *Serripes* Zone (3.6–2.6 Ma). The marine faunal assemblages in the *Tapes* and *Mactra* Zones are mainly boreal, but during deposition of the *Serripes* Zone, the fauna became greatly diversified with immigration of North Pacific molluscan species. These reached the North Atlantic at ca 3.6 Ma migrating through the Bering Strait and coeval with the final closure of the Central American Seaway. The closure changed partly the ocean current systems and induced a flow of surface water from the Pacific through the Bering Strait and into the Arctic Ocean and brought a tide of Pacific marine invertebrates into the North Atlantic. Plant fossils recovered from the Tjörnes beds originate from three localities. Sediments exposed at the Egilsgjóta (4.3–4.2 Ma) and Reká (4.2–4.0 Ma) localities are part of the *Tapes* Zone while those from Skeifá (3.9–3.8) belong to the *Mactra* Zone. The fossil flora does not show a distinct change from the oldest to the youngest sediments, but marks the last occurrence of warm temperate plant taxa in Iceland (*Tsuga, Ilex, Pterocarya,* large-leaved *Rhododendron, Trigonobalanopsis*). Relatively long-lasting warm conditions during the Pliocene were caused by the final closure of the Central American Seaway that started at around 5 Ma and the subsequent intensification of the Gulf Stream that brought warm water into the northern North Atlantic. A short cold spell at around 3.4 Ma as indicated by a shift in the oxygen isotope composition of fossil bivalves may reflect the first major glaciation in southeastern Greenland.

## 10.1 Introduction

On the western side of the Tjörnes Peninsula, northern Iceland (Fig. 10.1a, b), a 500 m thick sequence of fossiliferous marine and terrestrial sedimentary rocks and a few lavas, the Tjörnes beds, rest unconformably on Miocene lavas dated to 9–8 Ma (Aronson and Saemundsson 1975). The informal lithostratigraphic term 'Tjörnes beds' has traditionally been used to designate the sedimentary rock units between

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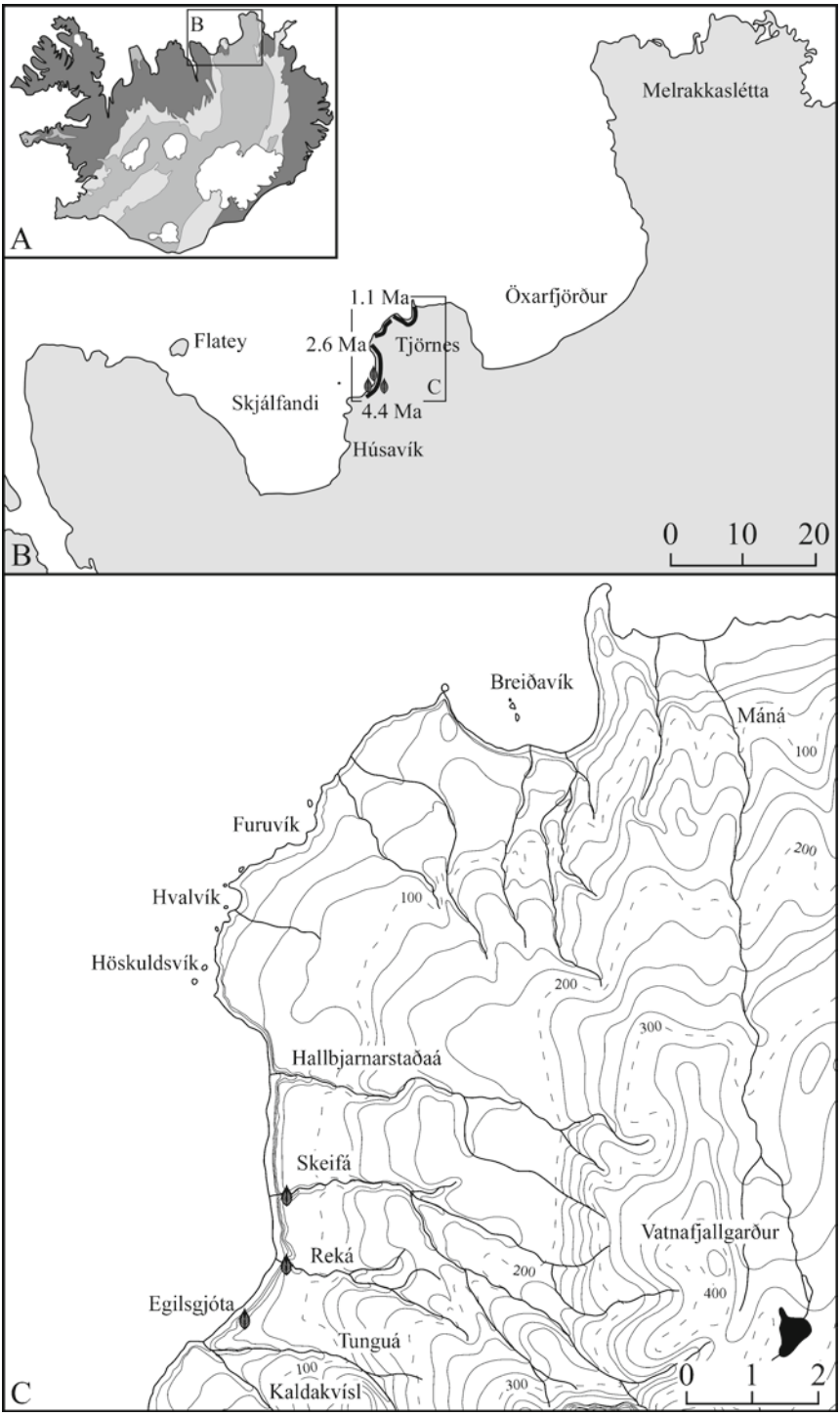



**Fig. 10.1** Map showing fossiliferous localities of the Tjörnes beds. (**a**) bedrock geology (see Fig. 1.10 for explanation) (**b**) extension of sedimentary rock formations, note that sediments

the Kaldakvísl and Höskuldsvík basaltic lavas on the Tjörnes Peninsula (Fig. 10.1b). The oldest part of the Tjörnes beds has been dated to about 4.4 Ma and the basaltic lavas capping the uppermost units is about 2.6 Ma (Albertsson 1976, 1978).

The exploration of the Tjörnes beds dates back to the middle and late eighteenth century, when the Icelandic naturalist Eggert Ólafsson (1749, 1772) first mentioned the Hallbjarnarstaður locality and noted some extinct molluscan species. Comprehensive geological and palaeontological studies of the Tjörnes beds commenced only much later, after the mid-nineteenth century. Winkler (1863), Paijkull (1867), Mörch (1871), Johnstrup (1877), Gardner (1885) and Harmer (1914–1925) studied mainly marine fossils. These authors speculated about palaeo-sea surface temperatures and correlated the Tjörnes beds with the more southern Pliocene Craig Formation in England and corresponding formations in continental Europe. Subsequently, Schlesch (1924) pointed out that the fauna had a more distinct northern character than the English and continental European formations. He also suggested that the climate had undergone some changes during deposition from the oldest to the youngest part of the beds.

Thoroddsen (1902) was the first who systematically studied the geology of the entire Tjörnes Peninsula and Bárðarson (1925) provided a detailed stratigraphic framework for the Tjörnes beds that is still in use. According to Bárðarson, the lignites and associated sandstones accumulated on land and in fresh water lakes, close to the shoreline. He considered the marine deposits to be mainly shallow water to littoral in origin and divided the Tjörnes beds into 25 distinct shell-bearing units, which he numbered 1–25, and ten terrestrial or transitional units designated as A–J (Fig. 10.2). Furthermore, Bárðarson grouped all units into three biozones, the *Tapes* Zone, the *Mactra* Zone and the *Serripes* Zone. He considered the three biozones to be of Pliocene age. Áskelsson (1935) also studied the fossiliferous Tjörnes beds, and in 1960, he compared their fauna with the sedimentary xenolith-fauna in Skammidalur, South Iceland, and suggested that the *Serripes* Zone should be Early Pleistocene in age (Áskelsson 1960).

Later, Durham and MacNeil (1967) used the fauna of the Tjörnes beds to reconstruct faunal migrations between the Pacific and Atlantic Oceans. Strauch (1963, 1972) studied selected molluscan genera of the Tjörnes beds and their depositional environments. He suggested that the beds were mainly deposited in a fjord open to the north with a sediment supply from the south. The palaeoecology of the Tjörnes beds and their relationship to the North Sea basin were assessed by Norton (1975), and the Tjörnes faunal assemblages were studied by Gladenkov et al. (1980).

Estimates of sea surface temperatures (SST) during deposition of the Tjörnes beds based on marine molluscs (Schwarzbach 1955; Schwarzbach and Pflug 1957) suggested a maximum SST 5°C warmer than today. Cronin (1991) determined similar SST values, based on the ostracod fauna of the Tjörnes beds comprised of several thermophilic genera which do not live in Icelandic waters at present. More recently, Buchardt and Símonarson (2003) analysed oxygen isotope compositions of the long-ranging bivalve species *Arctica islandica* (L.) that occurs throughout almost the

**Fig. 10.1** (continued) are getting younger from south to north, (**c**) Egilsgjóta, Reká and Skeifá localities (Geological background modified after Jóhannesson and Sæmundsson 1989; altitudinal lines from Landmælingar Íslands 1990). Scale bar in kilometres

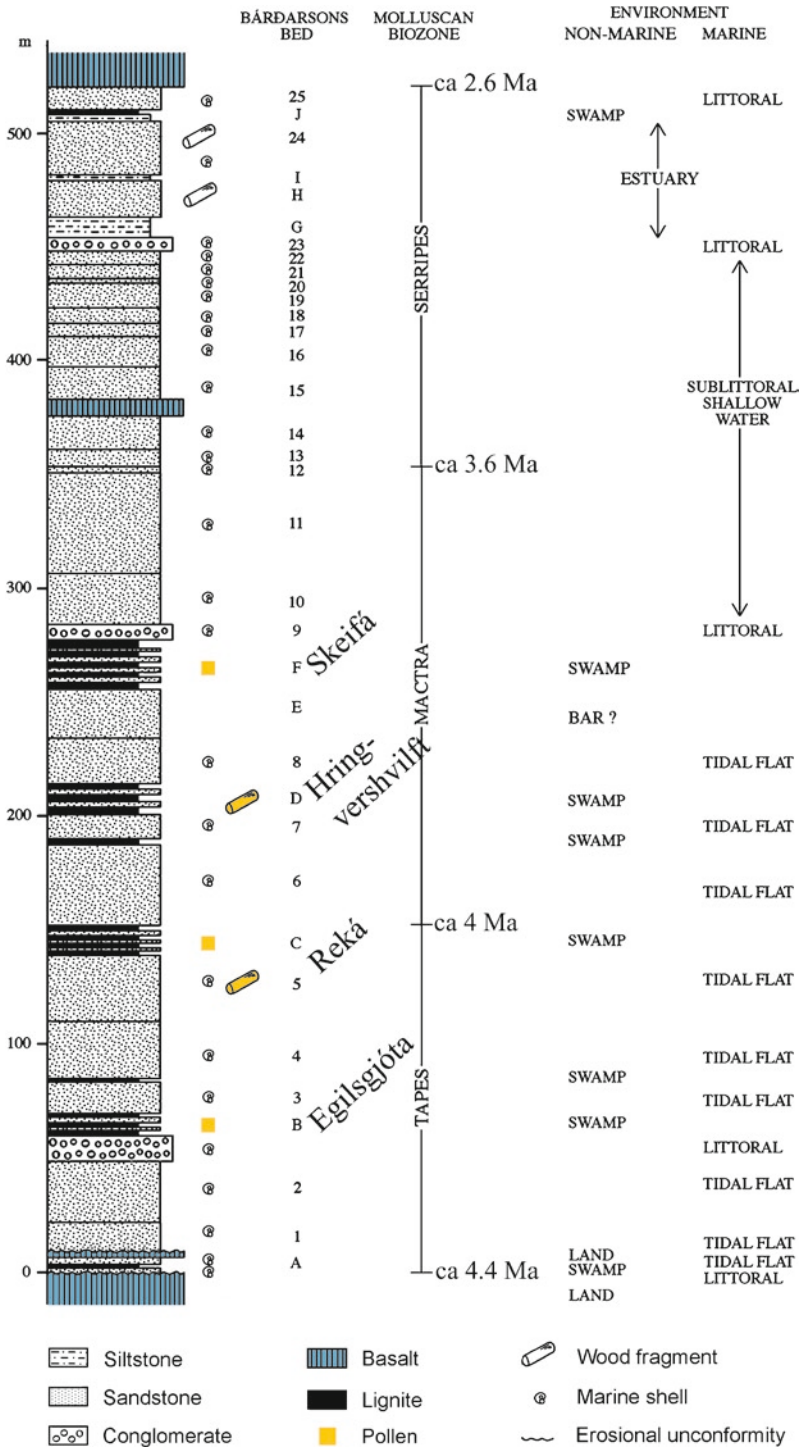



**Fig. 10.2** Generalized lithostratigraphic section of the Tjörnes Beds (After Buchardt and Símonarson 2003) indicating stratigraphic subdivisions of Bárðarson (1925) and marine environments). *Yellow squares* refer to plant fossil localities investigated for the present study, *yellow wood symbols* to localites studied by Löffler (1995)

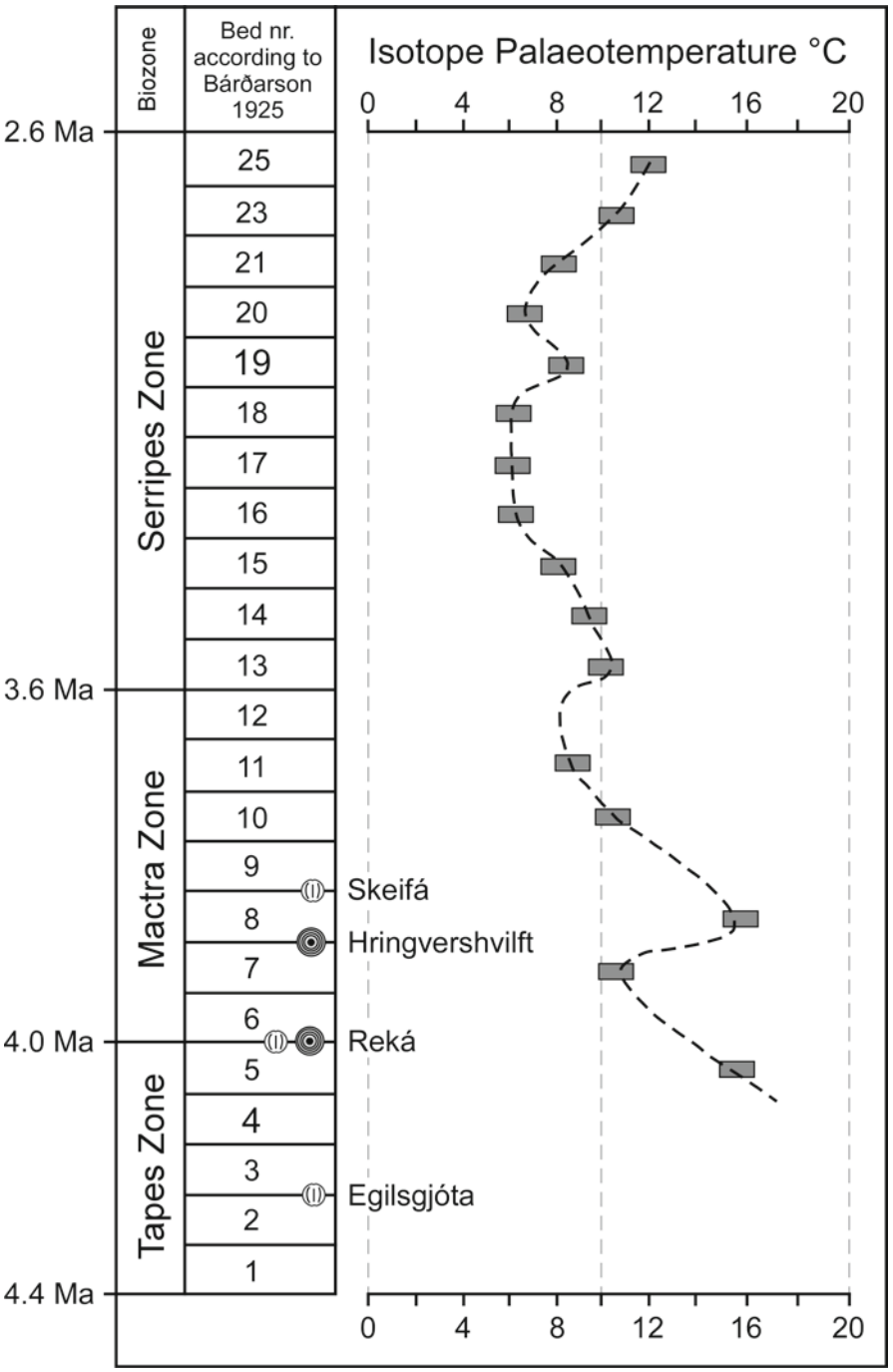



**Fig. 10.3** Isotope palaeotemperature curve derived from shells of two species of bivalves (From Buchardt and Símonarson 2003). The approximate positions of plant fossil localities discussed in the text are indicated

entire section of the Tjörnes beds and the extinct species *Pygocardia rustica* (Sowerby). They interpreted the oxygen isotope signature as annual summer palaeotemperatures (sea surface temperatures; Fig. 10.3) and observed a gradual change from warm-water conditions during the deposition of the lower parts of the Tjörnes beds to cold-water conditions during various parts of the *Mactra* and *Serripes* Zones.

Plant fossils from the terrestrial units of the Tjörnes beds have not been studied comprehensively prior to the present study. An early report of plant remains by Windisch (1886a, b) included fossil wood, and the most thorough study to date has been undertaken by Akhmetiev et al. (1978).

## 10.2 Geological Setting and Taphonomy

The Tjörnes beds and the uppermost Kaldakvísl lava flows (below the beds) dip 5–15° to the northwest. The sedimentary rocks are exposed in river canyons and sea cliffs for about 6 km along the coastline (Fig. 10.1a, b) on the west side of the Tjörnes Peninsula (Bárðarson 1925; Einarsson et al. 1967). The bulk of the sedimentary rocks are made up of fossiliferous marine sandstones with intermittent terrestrial or transitional lignites and muddy sandstones.

Lavas in the Kaldakvísl area underlying the Tjörnes beds have yielded ages of 9.9 ± 1.8 and 8.6 ± 0.4 Ma and a thin basaltic lava flow in the lowermost parts of the Tjörnes beds was dated to 4.3 ± 0.17 Ma (Aronson and Saemundsson 1975; Albertsson 1976; Fig. 10.2). This suggests that the Tjörnes beds were formed much later than the Kaldakvísl lavas. To the south of the Kaldakvísl river, the Tjörnes beds (*Tapes* Zone) begin with sandstones and conglomerates containing marine and littoral epifaunal molluscs. North of the river, the Tjörnes beds rest on the eroded surface of the Kaldakvísl lavas. These lavas are overlain by thin lignite units that most probably accumulated in wetlands close to the coast. The sandstones overlying the lignites have infaunal molluscan assemblages that preferably lived in tidal flat areas. However, the scarcity of mudrocks indicates sedimentation in areas with a rather limited tidal range (today about 1.5 m for the mean spring tide, and 0.5 m for the mean neap tide in Northeast Iceland; Stefánsson 1962). After the outpouring of a thin subaerial lava sheet, tidal flat sands accumulated again and are overlain by a conglomerate containing littoral epifaunal molluscs, about 50 m from the bottom of the *Tapes* Zone. Subsequently the upper part of the *Tapes* Zone and the lower part of the *Mactra* Zone were deposited by alternating accumulation of tidal flat sediments and terrestrial sediments (lignites, Fig. 10.2) in wetlands close to the coastline. The pollen samples from Egilsgjóta and Reká (Fig. 10.1c) originate from these terrestrial units, and are considered to be ca 4.2 and 4.0 Ma, respectively. In the middle part of the *Mactra* Zone the cross-bedded sandstones and gravels dissected by current channels in bed E accumulated. They are almost devoid of marine fossils; very fragmented mollusc shells are found only in the lowermost part. This indicates the inner part of littoral bar deposits. The bed is overlain by a thick lignite seam and conglomerates with littoral epifaunal molluscs. No lignites are found in the upper part of the *Mactra* Zone and the lower part of the *Serripes* Zone consists

of alternating units of sand- and siltstones deposited in a shallow water sublittoral environment. Slightly below the middle part of the *Mactra* Zone, the samples from Skeifá (Figs. 10.1c and 10.2) were obtained from terrestrial sediments deposited at ca 3.8 Ma. Undated pillow lava slightly above the *Mactra/Serripes* boundary (Skeifá lava) is of reverse remanent magnetism and has been correlated to the Gilbert-Gauss reversal at ca 3.6 Ma (Einarsson et al. 1967). In the middle part of the *Serripes* Zone, conglomerate with littoral epifaunal molluscs appears again, overlain by alternating layers of sand- and mudstones apparently formed in an estuarian environment, as indicated by the mollusc fauna and fossil wood remains found in the sediments. A lignite bed rests on the estuarian series and the sedimentary Tjörnes sequence terminates in sandstone with littoral epifaunal molluscs.

## 10.3 Faunas, Floras, Vegetation, and Palaeoenvironments

### *10.3.1 Marine Faunas and Depositional Environments*

The marine faunas in the *Tapes* and *Mactra* Zones are mainly boreal with Atlantic affinities, whereas during the deposition of the *Serripes* Zone, the fauna diversified due to the immigration of Pacific and Arctic elements. Two distinct changes in molluscan species composition are recorded in the Tjörnes beds. The first one, in the middle part of the *Mactra* Zone, is clearly connected to environmental changes in the area from an intertidal or tidal flat environment to a more sublittoral one, as is also evident from the sedimentary rocks. Species typical of flat tidal areas such as *Venerupis* spp. gradually disappear from the record and *Spisula arcuata* (Sowerby) and *Arctica islandica* (L.) become prominent, reflecting shallow water immediately outside the tidal zone (Símonarson and Eiríksson 2008). The second faunal change at ca 3.6 Ma is entirely different and was not caused by changing environments in the Tjörnes area, but by the profound re-organisation of global circulation patterns at that time. As the Central American Seaway approached closure starting ca 5 Ma (Haug and Tiedemann 1998; Haug et al. 2004), water flow through the Bering Strait reversed from southward to its present northward direction (Marincovich 2000). The Bering Strait had first opened at 5.5–4.8 Ma (Marincovich and Gladenkov 1999) and the initial phase of weak migration of Pacific molluscs into the Arctic Ocean and northern North Atlantic took place when the sediments of the *Tapes* and *Mactra* Zones were deposited (4.4–3.6 Ma; Símonarson et al. 1998; Marincovich and Gladenkov 1999; Marincovich 2000). These include common species such as *Mytilus edulis* L., *Modiolus modiolus* (L.) and *Zirfaea crispata* (L.) considered to have migrated through the Bering Strait and the Arctic Ocean (cf. Durham and MacNeil 1967; Bárðarson 1925). Pliocene molluscan assemblages in the Tjörnes beds include up to 22% extinct species (Norton 1975), most of which were typical of the *Tapes* and *Mactra* Zones. The boreal-lusitanian[1] assemblages in the *Tapes*

[1] Lusitanian denotes the marine fauna in the region between the English Channel and the Canary Islands.

Zone and the boreal assemblages in the *Mactra* Zone have a distinct Atlantic character with only a few species of Pacific ancestry. At the boundary between the *Mactra* and the *Serripes* Zones, at about 3.6 Ma, the abrupt appearance of several boreal-subarctic molluscs of Pacific origin is recorded (Durham and MacNeil 1967; Einarsson et al. 1967; Eiríksson et al. 1990; Marincovich 2000). *Neptunea despecta* (L.), *Buccinum undatum* L., *Serripes groenlandicus* (Mohr), *Ciliatocardium ciliatum* (Fabricius), *Macoma calcarea* (Gmelin), *Hiatella arctica* (L.) and several other species of North Pacific origin migrated into the Arctic Ocean and the North Atlantic during the deposition of the *Serripes* Zone (Durham and MacNeil 1967). Some of these species have since then been among the dominants in arctic and subarctic assemblages in marine faunas in the North Atlantic area. This prominent faunal change was most probably triggered by the final closure of the Central American Seaway (Isthmus of Panama) that induced a flow of surface water from the Pacific through the Bering Strait and into the Arctic Ocean and brought a tide of Pacific molluscs to the North Atlantic around Iceland at ca 3.6 Ma (Backman 1979; Marincovich 2000). Overall, major faunal turnovers seen in the Tjörnes beds may reflect biogeographic changes rather than distinct climatic changes.

### *10.3.2 Floras and Palaeolandscapes*

In contrast to the continuous record of marine invertebrates, plant fossil evidence is restricted to episodes of deposition of terrestrial sediments in coastal environments. One exception is the occurrence of wood in marine sediments (Löffler 1995). Overall, the floras encountered in the three time slices 4.3–4.2 Ma (Egilsgjóta), 4.2–4.0 Ma (Reká; *Tapes* Zone) and 3.9–3.8 Ma (Skeifá; *Mactra* Zone) are highly similar. Dominant elements belong to Pinaceae, Betulaceae and Ericaceae among the woody plants. However, the flora of the Reká locality is almost twice as rich as the floras from the older and younger Egilsgjóta and Skeifá localities (Table 10.1). The much higher diversity of the flora of Reká is mainly due to the increased diversity of herbaceous plants (Table 10.1; Fig. 10.4). Taxa such as *Tsuga* and *Sciadopitys* have their last occurrence in Iceland in the Reká sediments, and, among the angiosperms, aff. Calycanthaceae and *Viscum* cf. *album* are restricted to this locality. However, other warmth-loving elements are restricted to the younger Skeifá locality (*Ilex* sp. 1), or are only found in Egilsgjóta and Reká (*Euphorbia, Pterocarya*) or Reká and Skeifá (*Trigonobalanopsis*). The genus *Acer* is represented in all three localities.

Löffler (1995) studied wood from two layers (beds 5 and D in Fig. 10.2). From Reká (bed 5), she reported wood of *Piceoxylon* with botanical affinities to *Larix*, and, among the angiosperms, *Ilicoxylon* (*Ilex*), *Alnoxylon* (*Alnus*), *Populoxylon* and a wood type with affinities to both *Quercus* and *Fagus*. While *Larix*, *Ilex* and *Alnus* are also present in the pollen record of Reká, the fagaceous wood could possibly correspond to the extinct Fagaceae *Trigonobalanopsis* documented from Reká by

**Table 10.1** Taxa recorded for the 4.3–3.8 Ma floras of Iceland

| Tjörnes Beds | 4.3–4.2 Ma Egilsgjóta | | | 4.2–4.0 Ma Reká | | | 3.9–3.8 Ma Skeifá | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Taxa | P | L | R | P | L | R | P | L | R | DM |
| Bryophyta | | | | | | | | | | |
| *Sphagnum* sp. | | | | + | | | | | | 1a |
| Equisetaceae | | | | | | | | | | |
| *Equisetum* sp. | | | | | + | | | + | | 1a |
| Lycopodiaceae | | | | | | | | | | |
| *Lycopodiella* sp. | | | | + | | | | | | 1a |
| *Lycopodium* sp. | + | | | + | | | + | | | 1a |
| aff. *Huperzia* sp. | | | | + | | | | | | 1a |
| Lycopodiaceae gen. et spec. indet. 1 | | | | + | | | | | | 1a |
| Selaginellaceae | | | | | | | | | | |
| *Selaginella* sp. | | | | + | | | | | | 1a |
| Osmundaceae | | | | | | | | | | |
| *Osmunda* sp. | + | | | + | | | + | | | 1a |
| Polypodiaceae | | | | | | | | | | |
| *Polypodium* sp. 1 | | | | + | | | | | | 1a |
| Polypodiaceae gen. et spec. indet. 1 | | | | + | | | + | | | 1a |
| Polypodiaceae gen. et spec. indet. 2 | | | | + | | | | | | 1a |
| Polypodiaceae gen. et spec. indet. 6 | | | | + | | | + | | | 1a |
| Incertae sedis – imassigned spores | | | | | | | | | | |
| Trilete spore, fam., gen. et spec. indet. 3 | + | | | | | | | | | 1a |
| Trilete spore, fam., gen. et spec. indet. 4 | + | | | | | | | | | 1a |
| Trilete spore, fam., gen. et spec. indet. 5 | | | | | | | + | | | 1a |
| Monolete spore, fam., gen. et spec. indet. 3 | + | | | | | | | | | 1a |
| Monolete spore, fam., gen. et spec. indet. 4 | + | | | + | | | + | | | 1a |

(continued)

**Table 10.1** (continued)

| Tjörnes Beds | 4.3–4.2 Ma Egilsgjóta | | | 4.2–4.0 Ma Reká | | | 3.9–3.8 Ma Skeifá | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Taxa | P | L | R | P | L | R | P | L | R | DM |
| Pinaceae | | | | | | | | | | |
| *Abies* sp. | + | | | + | | | + | + | | 2a |
| *Picea* sp. | + | | | + | | | + | + | | 2a |
| Pinus sp. 1 (Diploxylon type) | | | | + | | | + | | | 2a |
| *Larix* sp. | + | | | + | + | | + | + | + | 2a |
| *Tsuga* sp. 1 | | | | + | | | | | | 2a |
| Sciadopityaceae | | | | | | | | | | |
| *Scyadopitys* sp. | | | | + | | | | | | 2a |
| Apiaceae | | | | | | | | | | |
| Apiaceae gen. et spec. indet. 1 | + | | | + | | | | | | 1b |
| Apiaceae gen. et spec. indet. 6 | + | | | + | | | | | | 1b |
| Apiaceae gen. et spec. indet. 8 | + | | | + | | | + | | | 1b |
| Apiaceae gen. et spec. indet. 9 | | | | + | | | + | | | 1b |
| Aquifoliaceae | | | | | | | | | | |
| *Ilex* sp. 1 | | | | | | | + | | | 1b |
| Asteraceae | | | | | | | | | | |
| *Cirsium* sp. | | | | + | | | | | | 1a |
| Asteraceae gen. et spec. indet. 1 | | | | + | | | | | | 1a |
| Asteraceae gen. et spec. indet. 5 | + | | | | | | | | | 1a |
| Asteraceae gen. et spec. indet. 6 | + | | | + | | | + | | | 1a |
| Asteraceae gen. et spec. indet. 7 | | | | + | | | | | | 1a |
| Asteraceae gen. et spec. indet. 8 | | | | + | | | | | | 1a |
| Betulaceae | | | | | | | | | | |
| *Alnus cecropiifolia* | + | | | (+) | | | (+) | + | | 1a, 2a |
| *Alnus* aff. *viridis* | + | | | (+) | | | (+) | + | + | 1a |
| *Betula* sp. | + | | | + | | | | | + | 1a |
| Calycanthaceae | | | | | | | | | | |
| aff. Calycanthaceae | | | | + | | | | | | 1b |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Campanulaceae | | | | | | | |
| *Campanula* sp. | | | + | | | | 1b |
| Caryophyllaceae | | | | | | | |
| Caryophyllaceae gen. et spec. indet. 1 | + | | | | | | 1b |
| Caryophyllaceae gen. et spec. indet. 4 | + | | + | | + | | 1b |
| Caryophyllaceae gen. et spec. indet. 5 | + | | | | | | 1b |
| Chenopodiaceae | | | | | | | |
| Chenopodiaceae gen. et spec. indet. 3 | | | + | | | | 1b |
| Cyperaceae | | | | | | | |
| *Carex* sp. | | | | | | + | 1b |
| *Kobresia* sp. | | | + | | | | 1b |
| Ericaceae | | | | | | | |
| *Rhododendron* aff. *ponticum* | + | | + | | + | + | 1a?, 2a |
| *Rhododendron* sp. 2 | | | + | | | | 1a?, 2a |
| *Vaccinium* cf. *uliginosum* | | | | | | + | 1b |
| Ericaceae gen. et spec. indet. 4 | + | | | | | | 1b |
| Ericaceae gen. et spec. indet. 5 | | | + | | | | 1b |
| Ericaceae gen. et spec. indet. 6 | | | + | | | | 1b |
| Ericaceae gen. et spec. indet. 7 | | | + | | | | 1b |
| Euphorbiaceae | | | | | | | |
| *Euphorbia* sp. | + | | + | | | | sea water |
| Fagaceae | | | | | | | |
| *Trigonobalanopsis* sp. | | | + | | + | | 2b, 3 |
| Juglandaceae | | | | | | | |
| *Pterocarya* sp. | + | | + | | | | 2a |
| Haloragaceae | | | | | | | |
| *Myriophyllum* sp. 2 | | | + | | | | 1b |
| Liliaceae | | | | | | | |
| Liliaceae gen. et spec. indet. 5 | + | | | | + | | 2a |
| Menyanthaceae | | | | | | | |
| *Menyanthes* sp. | | | + | | | | 1b |

(continued)

**Table 10.1** (continued)

| Tjörnes Beds | 4.3–4.2 Ma Egilsgjóta | | | 4.2–4.0 Ma Reká | | | 3.9–3.8 Ma Skeifá | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Taxa | P | L | R | P | L | R | P | L | R | DM |
| Myricaceae | | | | | | | | | | |
| *Myrica* sp. | + | | | + | | | + | | | 1b |
| Onagraceae | | | | | | | | | | |
| *Epilobium* sp. | | | | + | | | | | | 1a |
| Plantaginaceae | | | | | | | | | | |
| *Plantago coronopus* | | | | + | | | | | | 1b |
| Poaceae | | | | | | | | | | |
| *Phragmites* sp. | | | | | + | | | + | | 1b, 2a |
| Poaceae gen. et spec. indet. 1 | | | | | | | + | | | 1b, 2a |
| Poaceae gen. et spec. indet. 3 | + | | | + | | | | | | 1b, 2a |
| Polygonaceae | | | | | | | | | | |
| *Rumex* sp. | | | | + | | | | | | 1b |
| *Persicaria* sp. 2 | | | | + | | | | | | 1b |
| *Polygonum viviparum* | + | | | + | | | + | | | 1b |
| Potamogetonaceae | | | | | | | | | | |
| *Potamogeton* sp. | | | | | | | + | | | 1b |
| Ranunculaceae | | | | | | | | | | |
| *Ranunculus* sp. 1 | | | | + | | | | | | 1b |
| *Ranunculus* sp. 2 | + | | | | | | | | | 1b |
| *Thalictrum* sp. 2 | | | | + | | | | | | 1b, 2a |
| Ranunculaceae gen. et spec. indet. 2 | + | | | + | | | + | | | 1b |
| Ranunculaceae gen. et spec. indet. 4 | + | | | | | | | | | 1b |
| Ranunculaceae gen. et spec. indet. 5 | + | | | + | | | | | | 1b |
| Rosaceae | | | | | | | | | | |
| *Filipendula* sp. | + | | | + | | | + | | | 1b |
| *Fragaria* sp. | + | | | + | | | + | | | 1b |
| *Potentilla* sp. 1 | + | | | | | | | | | lb |
| *Rubus* sp. | | | | + | | | | | | lb |
| *Sanguisorba* sp. | + | | | + | | | + | | | 1b, 2a |
| *Sorbus* aff. *aucuparia* | | | | | | | | + | | 1b |
| Rosaceae gen. et spec. indet. 11 | | | | | | | + | | | 1b |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Salicaceae | | | | | | | | | | |
| *Salix gruberi* | | | | | | | | | + | 1a |
| *Salix* sp. B (*S. arctica* type) | | | | | | | | | + | 1a |
| *Salix* sp. 5 | + | | | + | | | + | | | 1a |
| Sapindaceae | | | | | | | | | | |
| *Acer* sp. 1 | + | | + | | | | | | | 2a |
| *Acer* sp. 2 | | | + | | | + | | | | 2a |
| Sparganiaceae | | | | | | | | | | |
| *Sparganium* sp. | | | + | | | + | | | | 1b |
| Trochodendraceae | | | | | | | | | | |
| *Tetracentron atlanticum* | + | | + | | | | | | | 2a |
| Valerianaceae | | | | | | | | | | |
| aff. *Valeriana* sp. | + | | + | | | + | | | | 1a |
| Viscaceae | | | | | | | | | | |
| *Viscum* aff. *album* | | | + | | | | | | | 1b |
| Incertae sedis – Magnoliophyta | | | | | | | | | | |
| Monocotyledonae fam.et gen. indet. 1 | | | | | | + | | | | ? |
| Angiosperm fam. gen. et spec. indet. C | | | | | | | + | | | ? |
| Pollen type 24 | + | | | | | | | | | ? |
| Pollen type 25 | + | | | | | | | | | ? |
| Pollen type 26 | + | | | | | | | | | ? |
| Pollen type 27 | | | + | | | | | | | ? |
| Pollen type 28 | | | + | | | | | | | ? |
| Pollen type 29 | + | | + | | | | | | | ? |
| Pollen type 30 | | | | | | + | | | | ? |

*L* leafy axis, *A* fruit attached to leafy axis, *D* fruit dispersed, *RP* reproductive structure, + organ present, **+** original description of species based on this organ, (+) organ belonging to genus but uncertain to which of the species, (+) 2 indicating number of pollen types possibly belonging to the eponymous morphotaxon, *DM* dispersal mode: *1a* wind long distance (anemochory), *1b* bird long distance (endozoochory), *2a* wind short distance (anemochory), *2b* animals short distance (exozoochory), *3* dyschory

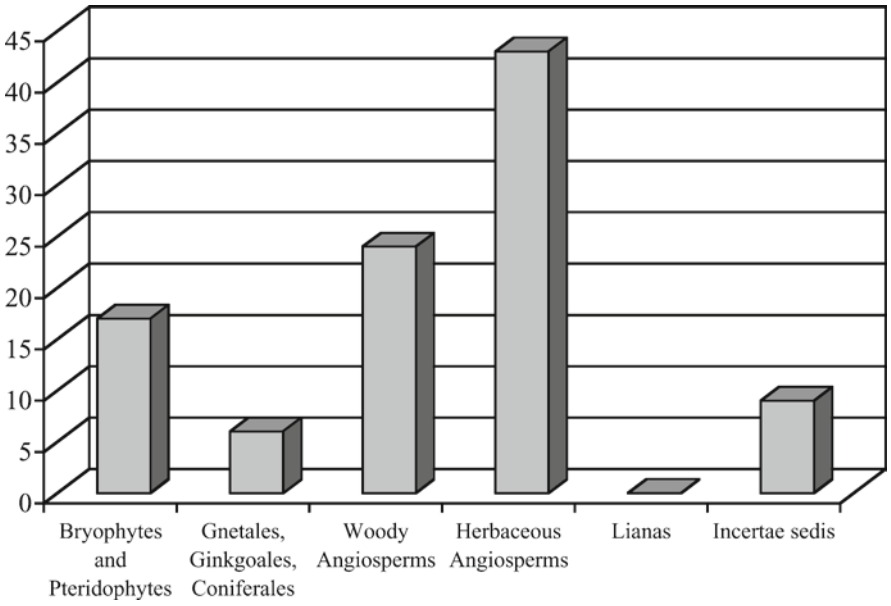



**Fig. 10.4** Distribution of life forms and higher taxa among the plants recovered from the Pliocene Tjörnes beds. Height of columns indicates number of taxa

pollen. Hringvershvilft is younger in age and corresponds to bed D, according to Bárðarson (1925). Stratigraphically, this layer is between the Reká and the Skeifá localities. Conifer wood is more diverse than in Reká with various *Piceoxylon* types with botanical affinities to *Picea glauca* (Moench) Voss and *Picea sitchensis* (Bong.) Carrière. In addition, wood resembling *Tsuga* and *Pseudotsuga* has been reported. The genus *Tsuga* is also present in the palynological record of Reká. Among the angiosperms, *Ilicoxylon* and *Populoxylon* are found; the latter resembles the wood of *Salix alba* L.

The vegetation in the Tjörnes area was diverse with aquatic vegetation and wetlands in coastal areas, where lagoons were temporally established. Wetlands were comprised of backswamp forests dominated by *Pterocarya*, Betulaceae, Myricaceae, *Salix* and Ericaceae and herbaceous plants, and swamp vegetation with fewer trees and a more diverse herbaceous flora (Figs. 10.5 and 10.6). Drier areas along the coast may have sustained coastal vegetation on sandy and rocky soils typically inhabited by plants such as Asteraceae, Polygonaceae or *Plantago coronopus* L. (Table 10.2). Well-drained levée forests and lowland forests were more diverse in woody species. *Acer* and *Pterocarya* may have been important canopy trees, whereas broadleaved deciduous and evergreen shrubs grew in the understorey. Towards the foothills and in the montane forests, conifers became more prominent. The montane forests were dominated by various conifer species with evergreen *Rhododendron* and small-leaved Ericaceae in the understorey (Fig. 10.7). Apart from wetlands and forests on well-drained soils, meadows played an important role in the landscape.

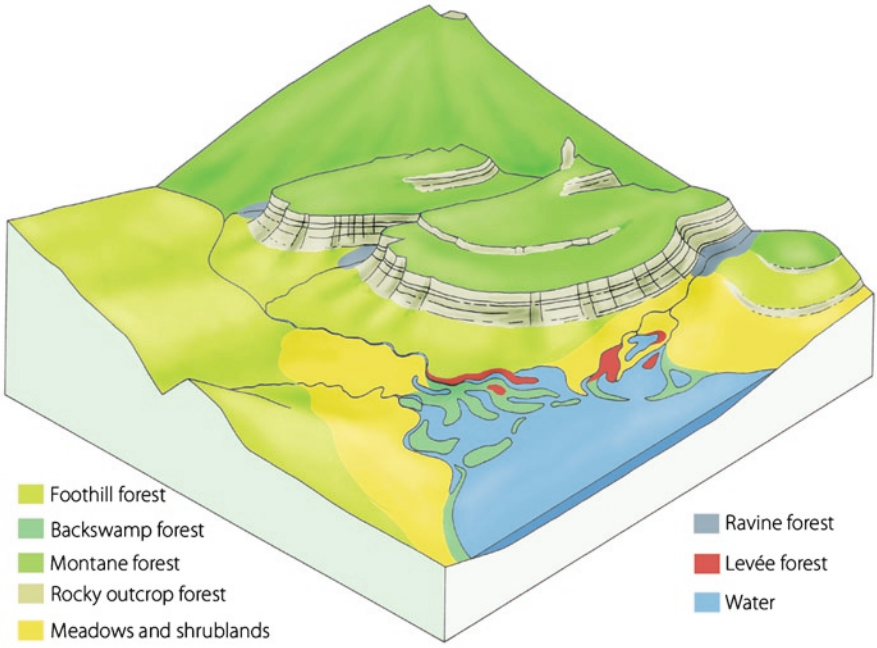



**Fig. 10.5** Schematic block diagram showing palaeo-landscape and vegetation types for the Pliocene of Iceland. See Table 10.2 for species composition of vegetation types

## 10.4 Climate of the Tjörnes Area During the Pliocene

### *10.4.1 Evidence from Marine Molluscs – Climatic Versus Biogeographic Signals*

Buchardt and Símonarson (2003) analysed the oxygen isotope composition of two species of bivalves, *Arctica islandica* (L.) and *Pygocardia rustica* (Sowerby) spanning a stratigraphical range from the middle part of the *Tapes* Zone to the upper part of the *Serripes* Zone (ca 4.2–2.6 Ma). They interpreted changes in isotope composition as proxies for palaeotemperatures. A gradual change was seen from warm-water conditions during the deposition of the lower part of the Tjörnes beds to more cold-water conditions in the middle part of the *Serripes* Zone and then again warm-water towards the upper parts of the *Serripes* Zone (Fig. 10.3). The coldest interval found in the middle part of the *Serripes* Zone at ca 3.4 Ma showed a calculated isotope sea temperature close to 5°C, which is similar to present, while temperatures at the top would have been between 11°C and 12°C.

The cold isotope signal at ca 3.4 Ma coincides well with the first large ice-rafted debris (IRD) peak recorded from ODP site 918, western Irminger Basin, southeast Greenland (St. John and Krissek 2002). Regional glaciation in southern Greenland




**Fig. 10.6** Schematic transect of a lowland riparian forest with well-drained elevated areas sustaining mixed hardwood forest

**Table 10.2** Vegetation types and their components during the Pliocene of Iceland

**Vegetation types 4.3–3.8 Ma**

**Aquatic vegetation**
- *Osmunda* sp.
- *Filipendula* sp.
- Liliaceae
- *Menyanthes* sp.
- *Myriophyllum* sp.
- *Phragmites* sp.
- *Potamogeton* sp.
- *Sparganium* sp.

**Backswamp forests and temporally flooded lake margin**
- *Equisetum* sp.
- *Osmunda* sp.
- *Polypodium* sp. 1
- Polypodiaceae gen. et spec. indet 1, 2, 6
- *Alnus cecropiifolia*
- *Betula* sp.
- *Carex* sp.
- Ericaceae gen. et spec. indet. 4-7
- *Myrica* sp.
- *Phragmites* sp.
- *Pterocarya* sp.
- *Salix gruberi*
- *Vaccinium* cf. *uliginosum*
- *Viscum* aff. *album*

**Swamp vegetation**
- *Osmunda* sp.
- *Sphagnum* sp.
- Apiaceae gen. et spec. indet. 1, 6, 8, 9
- *Alnus* aff. *viridis*
- *Alnus cecropiifolia*
- *Betula* sp.
- *Carex* sp.
- Chenopdiaceae gen. et spec. indet. 3
- *Cirsium* sp.
- *Epilobium* sp.
- *Filipendula* sp.
- *Kobresia* sp.
- Liliaceae
- *Menyanthes* sp.
- *Myrica* sp.
- *Persicaria* sp. 2
- *Phragmites* sp.
- Poaceae gen. et spec. indet. 1, 3
- *Rubus* sp.
- *Salix gruberi*
- *Vaccinium* cf. *uliginosum*
- aff. *Valeriana* sp.

**AZONAL VEGETATION**

**Levée and well-drained lowland forests and lake margins**
- Polypodiaceae gen. et spec. indet 1, 2, 6
- *Acer* sp. 1, 2
- *Alnus cecropiifolia*
- aff. Calycanthaceae
- Ericaceae gen. et spec, indet. 4-7
- *Ilex* sp. 1
- *Pterocarya* sp.
- *Rhododendron* aff. *ponticum*
- *Salix gruberi*
- *Viscum* aff. *album*

**Montane forests**
- Polypodiaceae gen. et spec. indet 1, 2, 6
- *Larix* sp.
- *Picea* sp.
- *Pinus* sp. 1
- *Scyadopitys* sp.
- *Tsuga* sp. 1
- *Betula* sp.
- Ericaceae gen. et spec. indet. 4-7
- *Rhododendron* aff. *ponticum*
- *Rhododendron* sp. 2
- *Sorbus* aff. *aucuparia*

**Foothill forests**
- *Abies* sp.
- *Picea* sp.
- *Acer* sp. 1, 2
- *Alnus cecropiifolia*
- *Betula* sp.
- *Ilex* sp. 1
- *Rhododendron* aff. *ponticum*
- *Rhododendron* sp. 2
- *Tetracentron atlanticum*
- *Trigonobalanopsis* sp.

**Rocky outcrop forests**
- aff. *Huperzia* sp.
- *Lycopodiella* sp.
- *Lycopodium* sp.
- *Pinus* sp. 1
- Asteraceae gen. et spec. indet. 1, 5-8
- *Campanula* sp.
- Ericaceae gen. et spec. indet. 4-7
- Poaceae gen. et spec. indet. 1, 3
- *Polygonum viviparum*
- *Potentilla* sp. 1
- *Sanguisorba* sp.
- *Sorbus* aff. *aucuparia*
- *Thalictrum* sp. 2
- aff. *Valeriana* sp.

**ZONAL VEGETATION**

(continued)

**Table 10.2** (continued)

| **Vegetation types 4.3–3.8 Ma** | | | |
|---|---|---|---|
| **Meadows and shrublands** | *Carex* sp. | *Potentilla* sp. 1 | **Coastal vegetation** |
| Aff. *Huperzia* sp. | Caryophyllaceae gen. et spec. indet. 1, 4, 5 | Ranunculaceae gen. et spec. indet. 2, 4, 5 | Asteraceae gen. et spec. indet. 1, 5-8 |
| *Equisetum* sp. | Chenopdiaceae gen. et spec. indet. 3 | *Ranunculus* sp. 1, 2 | Chenopodiaceae gen. et spec. indet. 3 |
| Lycopodiaceae gen. et spec. indet. 1 | *Cirsium* sp. | Rosaceae gen. et spec. indet. 11 | *Epilobium* sp. |
| *Lycopodiella* sp. | *Epilobium* sp. | *Rumex* sp. | *Euphorbia* sp. |
| *Lycopodium* sp. | Ericaceae gen. et spec. indet. 4-7 | *Salix* sp. B (‘*S. arctica*’ type) | *Kobresia* sp. |
| Polypodiaceae gen. et spec. indet. 1, 2, 6 | *Filipendula* sp. | *Sanguisorba* sp. | *Persicaria* sp. 2 |
| *Polypodium* sp. 1 | *Fragaria* sp. | *Sorbus* aff. *aucuparia* | *Plantago coronopus* |
| *Alnus* aff. *viridis* | *Kobresia* sp. | *Thalictrum* sp. 2 | *Polygonum viviparum* |
| Apiaceae gen. et spec. indet. 1, 6, 8, 9 | Liliaceae gen. et spec. indet. 5 | *Vaccinium* cf. *uliginosum* | *Rumex* sp. |
| Asteraceae gen. et spec. indet. 1, 5-8 | *Myrica* sp. | aff. *Valeriana* sp. | |
| *Betula* sp. | *Persicaria* sp. 2 | | |
| *Campanula* sp. | *Polygonum viviparum* | | |
| **ZONAL VEGETATION** | | | |
| The palaeoecology of fossil species is reconstructed from their sedimentological context and ecology of modern analogues | | | |

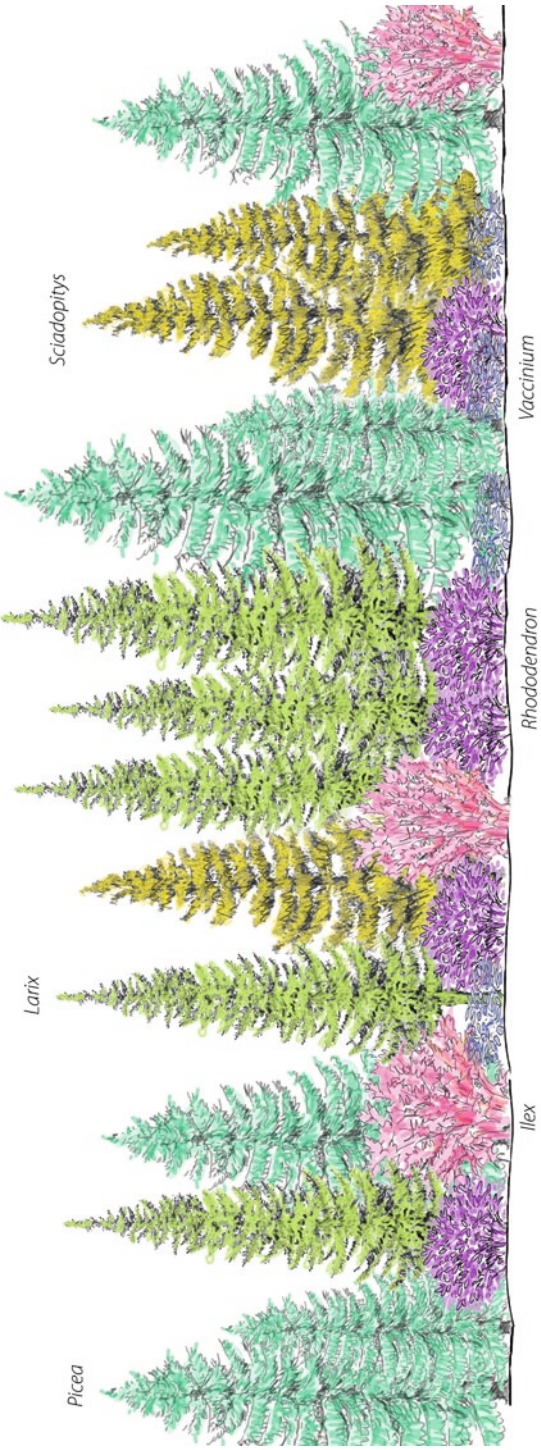



**Fig. 10.7** Schematic transect of montane conifer forest with evergreen shrubs in the understorey

may have influenced water temperatures north of Iceland. Less pronounced shifts in oxygen isotope composition in the seawater north of Iceland recorded for the period ca 4.2–2.6 Ma may also reflect the establishment of the modern current system. Today, the cold euhaline East Icelandic Current is a southeast flowing branch of the East Greenland Current that meets warmer Atlantic waters off the northeast coast of Iceland (see Chap. 1, Fig. 1.4). Mixing of these currents at various degrees may have strongly affected SST.

The arrival of potentially cold-water molluscs of Pacific origin in the lowermost part of the *Serripes* Zone occurred prior to the main cooling of the seas around Iceland. Among the first species to migrate into the North Atlantic from the Pacific were those shallow water and littoral species that reached Iceland during the deposition of the *Tapes* and *Mactra* Zones of the Tjörnes beds. Species that arrived at the boundary between the *Mactra* and *Serripes* Zones were mainly sublittoral. Although they display a more boreal-subarctic distribution than the species in the *Tapes* and *Mactra* Zones, they do not indicate decreasing sea temperatures in the Tjörnes area and the North Atlantic. Migration must have happened when the Arctic Ocean was ice-free and warmer than at present, as some of the migrating species no longer distribute that far north, e.g. *Neptunea decemcostata* (Say), *Hiatella arctica* (L.) (not *H. rugosa* (L.)) and *Panomya arctica* (Lamarck). However, sea temperatures in the Arctic Ocean during migration must have been some degrees lower than those in the North Pacific and North Atlantic, although the differences were not as pronounced as today. The Arctic Ocean probably acted as a filter to the migrating fauna, favouring species that were best adapted to the (cooler) conditions in the Arctic Ocean. These species dominate the assemblages at the boundary between the *Mactra* and *Serripes* Zones. Although the distinct faunal change could be interpreted as indicating a change in sea temperature, this is not supported by other data (Buchardt and Símonarson 2003; Fig. 10.3). The immigrating fauna appears not to reflect changes in sea temperatures in the Tjörnes area during deposition of the *Serripes* Zone, but probably temperature conditions further north in the Arctic Ocean.

### *10.4.2 Plant Evidence*

Based on the analysis of tree rings and tracheids of the Reká (4.2–4.0 Ma; *Tapes* Zone) wood samples, Löffler (1995) suggested a mild temperate climate with sufficient precipitation during the growing season and a relatively dry period during the winter. Winter temperatures most likely were above 0°C.

Wood samples from Hringvershvilft (ca 3.9 Ma; *Mactra* Zone) differ from those of Reká by a number of features (narrower growth rings, stronger fluctuations in growth ring width, presence of false tree rings, thicker walls of latewood tracheids, and smaller lumina in earlywood tracheids). Based on this, Löffler (1995) suggested slightly cooler conditions during formation of this bed (see the position of Hringvershvilft in Fig. 10.3). The presence of wood resembling *Picea sitchensis* and *Tsuga heterophylla* (Raf.) Sarg. may further point to conditions similar to the North American Pacific coast. The latter two species distribute from California to

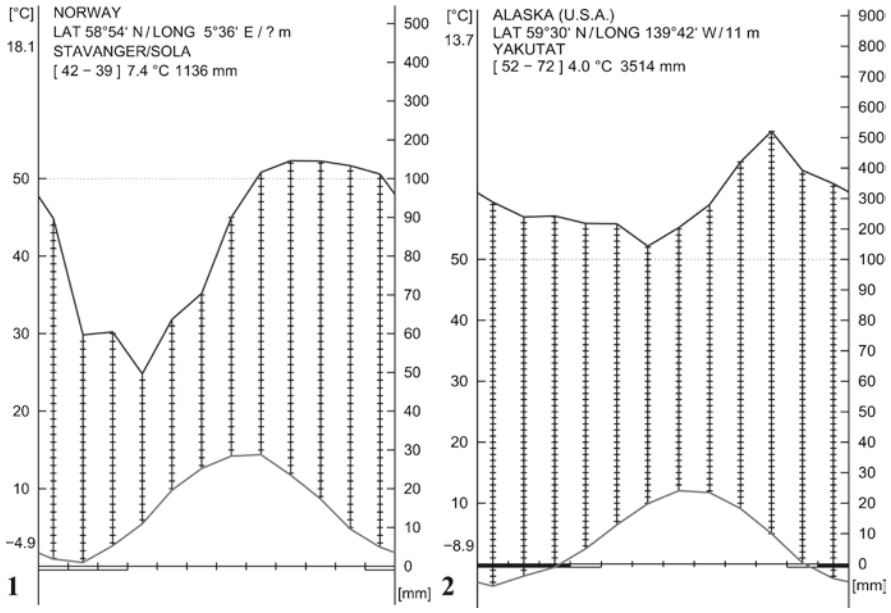



**Fig. 10.8** Climate diagrams resembling the climatic conditions inferred for the Pliocene of Iceland (Climate diagrams from Lieth et al. 1999). **1**. Stavanger, Cfb climate. **2**. Yakutat, Dfc climate (climate types according to Köppen, cf. Kottek et al. 2006)

southern Alaska (Fig. 10.8) and grow under various climate types including Mediterranean Csb and Csc climates, and humid temperate to cold Cfb, Cfc, and Dfc climates (Kottek et al. 2006).

*Ilex* occurs both in the palynological and the wood record of the Tjörnes beds. A potential modern analogue, the western Eurasian *Ilex aquifolium* L. is found from sea level up to 2,400 m a. s. l. from southern Scandinavia to northern Iran and northern Africa. It thrives under humid Cfa to Cfc climates, extending into Mediterranean Csa and Csb climates as part of the climatically favoured forests on northern slopes and in gorges. MAT for this species ranges from 7.2°C to18.2°C (data from Utescher and Mosbrugger 2009). *Rhododendron* aff. *R. ponticum* is most similar to the modern *Rhododendron ponticum* L. based on leaf and pollen morphology. The range of this species is generally similar to that of *Ilex aquifolium*. *Rhododendron ponticum* has a modern disjunct distribution with the subspecies *ponticum* occurring from the southern Black Sea coast to western Georgia, while subsp. *baeticum* (Boiss. et Reuter) Hand.-Mazz. has a small and scattered distribution on the southern and western Iberian Peninsula. A third isolated occurrence is known from central Lebanon, where *R. ponticum* var. *brachycarpum* Boiss. grows in *Pinus pinea* L. forests (Denk 2006). Based on the vertical and horizontal distribution of this species, a MAT range of 4.1–18.3°C can be estimated (Denk 2006). The current distribution of the species comprises various climate types (Cfa, Cfb, Csa, and Csb).

Overall, the plant fossil evidence indicates a cool Cfb climate for the *Tapes* Zone and the first half of the *Mactra* Zone, possibly similar to the modern climate of southern Norway (Fig. 10.8). Bárðarson's (1925) bed D may have been deposited under slightly cooler conditions. Based on the evidence from the marine record (see above) a cool temperate climate may have persisted until at least 3 Ma (see also Robinson 2009).

## 10.5 Comparison to Coeval Northern Hemispheric Floras and Faunas

From the Canadian High Arctic, rich macrofloras (fragments of leaves and twiglets, cones, fruits, and seeds) have been studied by Matthews and Ovenden (1990) and Fyles et al. (1994). The high latitude Pliocene Beaufort Formation on Banks Island has a stratigraphic range from 5 to 3 Ma. As in the Icelandic Tjörnes beds, no substantial change of vegetation can be seen during this interval (cf. horizons A to 73 of the Beaufort Formation, Appendix 10.1). Overall, the flora from the Beaufort Formation is similar to the Icelandic one. Interestingly, however, taxa that had their last occurrence in Iceland in the Middle and early Late Miocene (*Comptonia, Cornus, Decodon*) are rather common throughout the entire sequence in the Beaufort Formation. On the other hand, *Sciadopitys*, which has its last record in Iceland in the Tjörnes beds, is not found in the Beaufort Formation. Fossil representatives of *Comptonia* and *Sciadopitys* most likely belonged to different lineages than the single modern species of these genera and fossil representatives from Arctic regions may have had different climatic requirements than their modern relatives. Hence, their presence or absence in a flora may not be indicative of a particular climate. The flora from the Beaufort Formation at Ballast Brook is indicative of a cool temperate climate based on the presence of large-leaved Betulaceae and *Nymphaea*.

Lagoe and Zellers (1996) estimated Late Tertiary climatic changes in the eastern Gulf of Alaska using geological and palaeontological evidence from the 7 km thick Miocene to Pliocene Yakataga Formation. Planktic and benthic foraminiferal biofacies indicate a first cooling after ca 5.3 Ma (subarctic surface waters) followed by a warming at ca 4.2 Ma (temperate surface waters). The interval 4.2 to 3.5–3 Ma (roughly corresponding to the upper part of the *Tapes* Zone and the *Mactra* and possibly *Serripes* Zones) was relatively warm based on lithologic evidence (little ice-rafted material) and planktic foraminifera. This second interval corresponds to what has been called the Mid-Pliocene Warming event (Dowsett et al. 1996; Raymo et al. 1996; Robinson 2009).

For the Canadian High Arctic and Alaska, both evidence from plant fossils (Matthews and Ovenden 1990; Fyles et al. 1994) and geological and palaeontological evidence as used by Lagoe and Zellers (1996) do not resolve the distinct Pliocene climate fluctuations as seen in the isotopic signal of marine shells (cf. Kennett 1986; Buchardt and Símonarson 2003). Evidence from plant macrofossils and pollen and spores as used for the present study does not clearly reflect marked cooling

after deposition of the Egilsgjóta sediments. The pattern seen in taxa that persisted from the Egilsgjóta to the Reká locality and then disappeared from the fossil record (*Euphorbia* sp., *Pterocarya* sp., *Acer* sp. 1 and *Tetracentron atlanticum*) may be explained by continued cooling after deposition of the Reká sediments (Fig. 10.3). However, it may also be a sampling artefact. The signal captured in anatomical features of fossil wood from the Reká and Hringvershvilft localities (Löffler 1995) appears to be more sensitive to small-scale climate shifts as also recorded in Buchardt and Símonarson (2003) curve.

In Central Europe, the period ca 4.5–4 Ma (late Early Pliocene) coincides with a climatic optimum in which Mixed Mesophytic forests with several warmth-loving elements (evergreen Lauraceae, *Symplocos*, Theaceae etc.) still persisted (Mai and Walther 1988; Hably and Kvaček 1997). Apart from the generally warm character, Europe was climatically not uniform. From the latest Early Pliocene of northwestern Italy (Ca' Viettone succession, Martinetto 2001), a conspicuously rich palaeoflora is known that contains close to 50% exotic genera. This flora is rich in *Symplocos* species and Theaceae. For the early Late Pliocene (ca 3.6 Ma) of northern Italy, Martinetto (2001) did not find evidence of climatic fluctuations based on fruits, seeds, leaves and pollen. At the R.D.B. Quarry locality (Villafranca d'Asti), the whole succession is dominated by remains of *Taxodium* and *Glyptostrobus,* suggesting a coastal swamp in a deltaic plain. This flora does not contain *Symplocos* that appears to have its last occurrence in northern Italy around the boundary of the Early/Late Pliocene.

A number of exotic taxa are found at this Late Pliocene locality that are restricted to Middle Miocene floras in Iceland (*Glyptostrobus*, *Sequoia*, *Alnus gaudinii*, *Liriodendron*, *Magnolia*, *Sassafras*). In addition, taxa that never reached Iceland are present in the succession (e.g. *Ficus*, *Meliosma*, *Nyssa*, *Toddalia*, *Zelkova*). A less exotic flora from Germany (ca 3.6–2.6 Ma, Willershausen, Knobloch 1998) is still much richer than the Icelandic Pliocene floras. Typical elements of the Willershausen flora also found in Middle Miocene floras of Iceland are *Fagus, Liriodendron, Sassafras, Cercidiphyllum, Tilia, Aesculus, Betulaceae, Rosaceae,* various lobed oaks and species of *Acer*. Other taxa (*Parrotia, Liquidambar*) were characteristic elements in Miocene and Pliocene sediments of Europe (Mai 1995).

In conclusion, most plant fossil evidence from sub-Arctic and Arctic areas and from Central and Southern Europe indicates relatively warm conditions without dramatic floristic changes from the middle Early to the latest Pliocene (cf. Chap.11).

## 10.6 Summary

This chapter reviews the palaeobiogeography and palaeoecology of the Pliocene Tjörnes Beds (4.4–2.6 Ma) that were deposited when the Earth experienced a warm spell, termed the Mid-Pliocene Climatic Optimum. Marine molluscs have a continuous fossil record at Tjörnes and reflect a major biogeographic shift from distinct Atlantic affinities to mixed Atlantic-Pacific affinities after 3.6 Ma. This shift is less a consequence of changing climate than a result of the final closure of

the Isthmus of Panama and a major change in northern hemisphere ocean circulation. At the same time, isotope values from bivalve shells do indicate climatic fluctuations between 4.4 and ca 2.6. Plant fossils do not reflect marked climatic and environmental changes between ca 4.3 and 3.8 Ma. However, cooling between the deposition of sediments at Reká (4.2–4 Ma) and Hringvershvilft (ca 3.9 Ma), as indicated by oxygen isotopes, is also suggested by wood anatomical features. A comparison of high latitude floras from Iceland and Arctic Canada with mid-latitude floras from Italy and Central Europe clearly shows a marked latitudinal gradient for the period 5–2.6 Ma. In both regions, relatively warm floras persisted throughout the Pliocene and cooling was episodic rather than gradual. While global warm conditions during this period, as indicated by marine isotope data and geological evidence (Driscoll and Haug 1998; Haug et al. 2004), may not be seen as drastic changes in the palaeobotanical record, these last warm pulses before the onset of northern hemisphere glaciations allowed a temperate flora and vegetation to persist in Iceland until at least 3 Ma.

## Appendix 10.1

Floristic composition of the Pliocene Tjörnes beds of Iceland compared to contemporaneous assemblages from the North American Arctic.

| **Tjörnes beds floras [65° 36′ N, 17° 49′ W]** 4.4-3.8 Ma This study | |
|---|---|
| 2 | Equisetum sp. |
| 1 | aff. Huperzia sp. |
| 1 | Lycopodiaceae gen. et spec. indet. 1 |
| 1 | Lycopodiella sp. |
| 1 | Lycopodium sp. |
| 1 | Monolete spore, fam., gen. et spec. indet. 3 |
| 1 | Monolete spore, fam., gen. et spec. indet. 4 |
| 1 | Osmunda sp. |
| 1 | Polypodiaceae gen. et spec. indet. spp. |
| 1 | Polypodium sp. 1 |
| 1 | Selaginella sp. |
| 1 | Sphagnum sp. |
| 1 | Trilete spore, fam., gen. et spec. indet. spp. |
| 1, 3 | Abies sp. |
| 1-3 | Larix sp. |
| 1, 3 | Picea sp. |
| 1 | Pinus sp. 1 (Diploxylon type) |
| 1 | Scyadopitys sp. |
| 1 | Tsuga sp. 1 |
| 1 | Acer sp. 1 |
| 1 | Acer sp. 2 |
| 1-3 | Alnus aff. viridis |
| 1-3 | Alnus cecropiifolia |
| 1 | Angiosperm fam. gen. et spec. indet. C |
| 1 | Apiaceae gen. et spec. indet. spp. |
| 1 | Asteraceae gen. et spec. indet. spp. |
| 1, 2 | Betula sp. |
| 1 | aff. Calycanthaceae |
| 1 | Campanula sp. |
| 1 | Carex sp. |
| 1 | Caryophyllaceae gen. et spec. indet. spp. |
| 1 | Chenopodiaceae gen. et spec. indet. 3 |
| 1 | Cirsium sp. |
| 1 | Epilobium sp. |
| 1 | Ericaceae gen. et spec. indet. spp. |
| 1 | Euphorbia sp. |
| 1 | Filipendula sp. |
| 1 | Fragaria sp. |
| 1 | Ilex sp. 1 |
| 1 | Kobresia sp. |

(continued)

| | **Tjörnes beds floras** (continued) |
|---|---|
| 1 | Liliaceae gen. et spec. indet. 5 |
| 1 | Menyanthes sp. |
| 1 | Monocotyledonae fam.et gen. indet. 1 |
| 1 | Myrica sp. |
| 1 | Myriophyllum sp. 2 |
| 1 | Persicaria sp. 2 |
| 2 | Phragmites sp. |
| 1 | Plantago coronopus |
| 1 | Poaceae gen. et spec. indet. 1 |
| 1 | Poaceae gen. et spec. indet. 3 |
| 1 | Polygonum viviparum |
| 3 | Potamogeton sp. |
| 1 | Potentilla sp. 1 |
| 1 | Pterocarya sp. |
| 1 | Ranunculaceae gen. et spec. indet. spp. |
| 1 | Ranunculus sp. 1 |
| 1 | Ranunculus sp. 2 |
| 3 | Rhododendron aff. ponticum |
| 1 | Rhododendron sp. 2 |
| 1 | Rosaceae gen. et spec. indet. 11 |
| 1 | Rubus sp. |
| 1 | Rumex sp. |
| 3 | Salix gruberi |
| 1 | Salix sp. 5 |
| 3 | Salix sp. B (S. arctica type) |
| 1 | Sanguisorba sp. |
| 3 | Sorbus aff. aucuparia |
| 1 | Sparganium sp. |
| 1 | Tetracentron atlanticum |
| 1 | Thalictrum sp. 2 |
| 1 | Trigonobalanopsis sp. |
| 3 | Vaccinium cf. uliginosum |
| 1 | aff. Valeriana sp. |
| 1 | Viscum aff. album |

| | **Beaufort Formation at Ballast Brook, Banks Island Arctic Canada [ca 74°20′ N, 123°10′ W]** |
|---|---|
| | 5-3 Ma; Fyles et al., 1994 |
| | Site 9 Horizon A |
| 2 | **Abies sp.** |
| 2 | **Picea sp.** |
| 2 | **Pinus** undiff. |
| 2 | **Pinus** (Strobus) undiff. |
| 2 | **Alnus** incana type |
| 2 | **Alnus sp.** |
| 2 | Andromeda polifolia |
| 2 | Aracites globosa |
| 2 | **Betula sp.** |
| 2 | **Carex spp.** |
| 2 | **Chenopodium sp.** |
| 2 | *Cleome sp.* |
| 2 | Comptonia sp. |
| 2 | Decodon globosus type |
| 2 | Epipremnum crassum |
| 2 | **Menyanthes**(<2mm) |
| 2 | **Myrica** eogale type |
| 2 | **Myrica sp.** |
| 2 | Physocarpus sp. |
| 2 | **Potentilla sp.** |
| 2 | **Ranunculus** hyperboreus |
| 2 | **Rubus sp.** |
| | **Site 9** Horizon B |
| 2 | **Picea sp.** |
| 2 | **Alnus** incana type |
| 2 | Andromeda polifolia |
| 2 | Aracites globosa |
| 2 | Aralia sp. |
| 2 | **Betula sp.** |
| 2 | **Carex spp.** |
| 2 | *Cleome sp.* |
| 2 | Comptonia sp. |
| 2 | Cornus stolonifera type |
| 2 | Decodon globosus type |
| 2 | Hippuris sp. |
| 2 | **Menyanthes** (<2mm) |
| 2 | **Menyanthes trifoliata** |
| 2 | Microdiptera parva |
| 2 | *Microdiptera/Mneme type* |
| 2 | Nymphaea sp. |
| 2 | Nymphoides sp. |
| 2 | **Polygonum sp.** |
| 2 | **Potamogeton sp.** |
| 2 | **Potamogeton** bupleuroides type |
| 2 | **Potampogeton** filiformis type |
| 2 | **Potentilla** norvegica |
| 2 | **Potentilla** palustris |
| 2 | **Rubus sp.** |
| 2 | **Rumex sp.** |
| 2 | Verbenaceae |
| 2 | Viburnum sp. |

(continued)

**Beaufort Formation** (continued)

**Site 9** Horizon C

| | |
|---|---|
| 2 | **Larix sp.** |
| 2 | **Picea sp.** |
| 2 | Alisma-Sagittaria type |
| 2 | **Alnus** incana type |
| 2 | Andromeda polifolia |
| 2 | Aracites globosa |
| 2 | **Betula** arboreal type |
| 2 | **Carex spp.** |
| 2 | **Caryophyllaceae** |
| 2 | **Chenopodium sp.** |
| 2 | *Cleome sp.* |
| 2 | Comptonia sp. |
| 2 | Cornus stolonifera type |
| 2 | Decodon globosus type |
| 2 | Epipremnum crassum |
| 2 | Glyceria sp. |
| 2 | **Menyanthes trifoliata** |
| 2 | **Myrica** eogale type |
| 2 | Nuphar sp. |
| 2 | Nymphaea sp. |
| 2 | Nymphoides sp. |
| 2 | Physocarpus sp. |
| 2 | **Potamogeton sp.** |
| 2 | **Ranunculus** hyperboreus |
| 2 | **Ranunculus** lapponicus |
| 2 | **Rumex sp.** |
| 2 | Sambucus sp. |
| 2 | Scirpus sp. |
| 2 | **Sparganium sp.** |

**Site 9** Horizon 3

| | |
|---|---|
| 2 | **Bryophyta** |
| 2 | **Larix sp.** |
| 2 | **Picea sp.** |
| 2 | **Pinus** subsect. Eustrobi |
| 2 | Thuja sp. |
| 2 | **Tsuga sp.** |
| 2 | Aracites globosa |
| 2 | **Betula** apoda type |
| 2 | **Betula** arboreal type |
| 2 | Bidens cernua type |
| 2 | Bidens sp. |
| 2 | **Carex sp.** |
| 2 | **Chenopodium sp.** |
| 2 | *Cleome sp.* |
| 2 | Cornus stolonifera type |
| 2 | Decodon globosus type |
| 2 | Dulichium sp. |
| 2 | Eleocharis sp. |
| 2 | Hippuris sp. |
| 2 | **Myrica** eogale type |
| 2 | **Potamogeton sp.** |
| 2 | **Potentilla** palustris |
| 2 | **Ranunculus** hyperboreus |
| 2 | **Rumex sp.** |
| 2 | **Salix sp.** |
| 2 | *Spirematospermum wetzleri* |
| 2 | Viola sp. |

**Site 9** Horizon 4a

| | |
|---|---|
| 2 | **Bryophyta** |
| 2 | **Larix** cf. L. groenlandii |
| 2 | **Picea sp.** |
| 2 | **Pinus** subsect. Cembrae |
| 2 | **Alnus** crispa |
| 2 | **Betula sp.** |
| 2 | **Carex sp.** |
| 2 | Populus sp. |
| 2 | **Potentilla** norvegica |
| 2 | **Ranunculus** hyperboreus |
| 2 | **Ranunculus** lapponicus |
| 2 | **Salix sp.** |

**Site 9** Horizon 73

| | |
|---|---|
| 2 | **Larix sp.** |
| 2 | **Picea sp.** |
| 2 | **Pinus** densiflora/resinosa type |
| 2 | Thuja sp. |
| 2 | **Alnus sp.** |
| 2 | Andromeda polifolia |
| 2 | Aracites globosa |
| 2 | **Betula** arboreal type |
| 2 | **Carex sp.** |
| 2 | **Caryophyllaceae** |
| 2 | Chamaedaphne sp. |
| 2 | *Cleome sp.* |

(continued)

| | **Beaufort Formation** (continued) |
|---|---|
| 2 | Cornus stolonifera type |
| 2 | Decodon globosus type |
| 2 | Dulichium sp. |
| 2 | Epipremnum crassum |
| 2 | Hippuris sp. |
| 2 | **Menyanthes trifoliata** |
| 2 | **Myrica** eogale type |
| 2 | Nuphar sp. |
| 2 | Physocarpus sp. |
| 2 | **Ranunculus spp.** |
| 2 | **Rubus sp.** |
| 2 | **Rumex sp.** |
| 2 | **Salix sp.** |
| 2 | Sambucus sp. |
| 2 | Triglochin maritimum |
| 2 | Viola sp. |

Boldface indicates that the genus is present in the Tjörnes beds. Grey shading indicates that the genus is present in the younger Pleistocene or older Late Miocene formations. 1 = based on pollen, spores; 2 = based on leaves and/or fruit/seed fossils; 3 = based on leaf fossils

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## Explanation of Plates

**Plate 10.1** **1–2**. Tjörnes Peninsula, Tjörnes sediments, *Tapes* and *Mactra Zones* (ca 4.4–3.6 Ma). **1**. Sedimentary units of the Tapes Zone in upper half of photo (Egilsgjóta and Reká outcrops), and of the Mactra Zone in the lower half. **2**. Continuation of sedimentary units belonging to the Mactra zone (Skeifá outcrop). **3**. Egilsgjóta outcrop where the oldest pollen sample from Tjörnes originates. **4**. The complete Reká outcrop. **5**. Detail of the upper sedimentary unit at Reká showing lagoon and terrestrial sediments. **6**. Fine grained siltstones and lignite seems at Reká. **7**. Skeifá outcrop where the youngest Tjörnes plant fossils originate. **8**. Plant fossil bearing sedimentary units at Skeifá. **9–12**. Preservation of plant fossils in siltstone (**9**), sandstone (**10**, **11**) and diatomite (**12**)

**Plate 10.2** **1**. *Equisetum* sp., rhizome with nodules (IMNH 501). **2**. *Equisetum* sp. (S 116535). **3**. *Abies* sp., needle ( IMNH org 227). **4**. *Picea* sp. lower part of cone (IMNH 4196). **5**. *Larix* sp., part of branch with short lateral spur shoots (IMNH org 208). **6**. *Larix* sp., short shoot with several leaves (IMNH org 228). **7**. *Larix* sp., female cone (IMNH org 213). **8**. *Picea* sp., needle (IMNH 216). **9**. Cyperaceae/Poaceae, leaf fragments

**Plate 10.3** **1–3**. *Sphagnum* sp. **1**. Spore in SEM, proximal polar view showing trilete tetrad mark. **2**. Detail of spore surface. **3**. Spore in LM, proximal polar view. **4–6**. *Lycopodiella* sp. **4**. Spore in SEM, proximal polar view. **5**. Detail of spore surface. **6**. Spore in LM, oblique polar view. **7–9**. *Lycopodium* sp. **7**. Spore in SEM, distal polar view. **8**. Detail of spore surface. **9**. Spore in LM, equatorial view. **10–12**. *Huperzia* sp. **10**. Spore in SEM, distal polar view. **11**. Detail of spore surface. **12**. Spore in LM, proximal polar view showing trilete tetrad mark

**Plate 10.4** **1–3**. *Selaginella* sp. **1**. Spore in SEM, distal polar view. **2**. Detail of spore surface. **3**. Spore in LM. **4–6**. *Osmunda* sp. **4**. Spore in SEM, proximal polar view. **5**. Detail of spore surface. **6**. Spore in LM, proximal polar view showing tetrad mark. **7–9**. *Polypodium* sp. 1. **7**. Spore in SEM. **8**. Detail of spore surface. **9**. Spore in LM. **10–12**. Polypodiaceae gen. et spec. indet. 1. **10**. Spore in SEM, proximal polar view. **11**. Detail of spore surface. **12**. Spore in LM, proximal polar view showing monolete tetrad mark

**Plate 10.5** **1–3**. Polypodiaceae gen. et spec. indet. 2. **1**. Spore in SEM, distal polar view. **2**. Detail of spore surface. **3**. Spore in LM, proximal polar view showing trilete tetrad mark. **4–6**. Polypodiaceae gen. et spec. indet. 6. **4**. Spore in SEM, equatorial view. **5**. Detail of spore surface. **6**. Spore in LM, equatorial view. **7–9**. Trilete spore fam., gen. et spec. indet. 3. **7**. Spore in SEM, proximal polar view showing trilete tetrad mark. **8**. Detail of spore surface. **9**. Spore in LM, proximal polar view showing trilete tetrad mark. **10–12**. Trilete spore fam. gen. et spec. indet. 4. **10**. Spore in SEM, oblique proximal polar view. **11**. Detail of spore surface. **12**. Spore in LM, distal polar view

**Plate 10.6** **1–3**. Trilete spore fam. gen. et spec. indet. 5. **1**. Spore in SEM. **2**. Detail of spore surface. **3**. Spore in LM. **4–6**. Monolete spore fam. gen. et spec. indet. 3. **4**. Spore in LM, distal polar view. **5**. Detail of spore surface. **6**. Spore in LM, proximal polar view showing monolete tetrad mark. **7–9**. Monolete spore fam. gen. et spec. indet. 4. **7**. Spore in SEM, oblique distal polar view. **8**. Detail of spore surface. **9**. Spore in LM, equatorial view. **10–12**. Monolete spore fam. gen. et spec. indet. 4. **10**. Spore in SEM, proximal polar view showing monolete tetrad mark. **11**. Detail of spore surface. **12**. Spore in LM, proximal polar view

**Plate 10.7** **1–3**. *Abies* sp. **1**. Bisaccate pollen grain in SEM, oblique distal polar view. **2**. Detail of saccus surface. **3**. Bisaccate pollen grain in LM, oblique equatorial view. **4–6**. *Picea* sp. **4**. Bisaccate pollen grain in SEM, oblique equatorial view. **5**. Detail of pollen surface **6**. Bisaccate pollen grain in LM, oblique equatorial view. **7**. *Pinus* sp. 1 (Diploxylon type), bisaccate pollen grain in LM

**Plate 10.8** **1–3**. *Larix/Pseudotsuga* sp. **1**. Pollen grain in SEM, proximal polar view showing y-shaped impression mark. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, proximal polar view. **4–8**. *Tsuga* sp. 1. **4**. Monosaccate pollen grain in SEM, proximal polar view. **5**. Detail of pollen grain surface, proximal side. **6**. Monosaccate pollen grain in LM, polar view. **7**. Monosaccate pollen grain in SEM, distal polar view. **8**. Detail of pollen grain surface, distal side. **9–11**. *Scyadopitys* sp. **9**. Pollen in SEM. **10**. Detail of pollen grain surface. **11**. Pollen grain in LM

**Plate 10.9** **1–3**. Apiaceae gen. et spec. indet. 6. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4–6**. Apiaceae gen. et spec. indet. 1. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7–9**. Apiaceae gen. et spec. indet. 8. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view. **10–12**. Apiaceae gen. et spec. indet. 9. **10**. Pollen grain in SEM, equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, equatorial view

**Plate 10.10** **1–3**. *Ilex* sp. 1. **1**. Pollen in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4–6**. *Cirsium* sp. **4**. Pollen grain in SEM, polar view. **5**. Detail of pollen surface and structure. **6**. Pollen grain in LM, polar view. **7–9**. Asteraceae gen. et spec. indet. 1 (Tubuliflorae). **7**. Pollen grain in SEM, oblique equatorial view. **8**. Detail of pollen surface. **9**. Pollen in LM

**Plate 10.11** **1–3**. Asteraceae gen. et spec. indet. 5. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. pollen grain in LM, polar view. **4–6**. Asteraceae gen. et spec. indet. 6. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, oblique polar view. **7–9**. Asteraceae gen. et spec. indet. 7. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, oblique equatorial view. **10–12**. Asteraceae gen. et spec. indet. 8. **10**. Pollen in SEM, oblique equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, equatorial view

**Plate 10.12** **1**. *Alnus cecropiifolia*, large wide ovate leaf (MHH). **2**. *Alnus cecropiifolia*, part of elliptic leaf (S116539). **3**. *Alnus cecropiifolia*, large wide elliptic leaf (S116538). **4**. *Alnus* aff. *viridis*, obovate leaf. **5**. *Alnus* aff. *viridis*, female infructescences (IMNH org 221). **6**. *Betula* sp., winged seed

**Plate 10.13** **1–3**. *Alnus* sp. 1. **1**. Pollen grain in SEM, polar view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, polar view. **4–6**. *Alnus* sp. 3. **4**. Pollen grain in SEM, polar view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, polar view. **7–9**. *Betula* sp. **7**. Pollen grain in SEM, polar view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, polar view. **10–12**. aff. Calycanthaceae **10**. Pollen grain in SEM, equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, equatorial view

**Plate 10.14** **1–3**. *Campanula* sp. **1**. Pollen grain in SEM. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM. **4–6**. Caryophyllaceae gen. et spec. indet. 1. **4**. Pollen grain in SEM. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM. **7–9**. Caryophyllaceae gen. et spec. indet. 4. **7**. Pollen grain in SEM. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM. **10–12**. Caryophyllaceae gen. et spec. indet. 5. **10**. Pollen grain in SEM. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM

**Plate 10.15** **1–3**. Chenopodiaceae gen. et spec. indet. 3. **1**. Pollen grain in SEM. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM. **4–6**. *Kobresia* sp. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen in LM, equatorial view. **7–10**. *Rhododendron* sp. 1. (*R. ponticum* type). **7**. Tetrad in SEM. **8**. Detail of tetrad surface showing viscin thread. **9**. Detail of tetrad surface, mesocolpium area. **10**. Tetrad in LM

**Plate 10.16** **1**. *Rhododendron* aff. *ponticum*, large elliptic leaf (IMNH org 220). **2**. *Rhododendron* aff. *ponticum*, medium sized narrow elliptic leaf (IMNH org 219). **3**. *Rhododendron* aff. *ponticum*, small narrow elliptic leaf (S 116535). **4**. Detail of Fig. 3. showing secondary venation. **5**. *Carex* sp., axis with leaves and inflorescence (IMNH org 200). **6**. *Carex* sp., inflorescence (IMNH org 202)

**Plate 10.17** **1–3**. *Rhododendron* sp. 2. **1**. Tetrad in SEM. **2**. Detail of tetrad surface showing part of viscin thread. **3**. Tetrad in LM. **4–6**. Ericaceae gen. et spec. indet. 4. **4**. Tetrad in SEM. **5**. Detail of tetrad surface. **6**. Tetrad in LM. **7–9**. Ericaceae gen. et spec. indet. 5. **7**. Tetrad in SEM. **8**. Detail of tetrad surface. **9**. Tetrad in LM

**Plate 10.18** **1–3**. Ericaceae gen. et spec. indet. 6. **1**. Tetrad in SEM. **2**. Detail of tetrad surface. **3**. Tetrad in LM. **4–6**. Ericaceae gen. et spec. indet. 7. **4**. Tetrad in SEM. **5**. Detail of tetrad surface. **6**. Tetrad in LM. **7–9**. *Euphorbia* sp. **7**. Pollen grain in SEM, oblique polar view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, oblique polar view

**Plate 10.19** **1–3**. *Trigonobalanopsis* sp. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4–6**. *Trigonobalanopsis* sp. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7–9**. *Pterocarya* sp. **7**. Pollen in SEM, polar view. **8**. Detail of pollen grain surface. **9**. Pollen in LM, polar view. **10–12**. *Myriophyllum* sp. 2. **10**. Pollen grain in SEM. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM

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**Plate 10.21** **1–3**. *Epilobium* sp. **1**. Pollen grain in SEM, polar view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, polar view. **4–6**. *Plantago coronopus*. **4**. Pollen grain in SEM. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM. **7–9**. Poaceae gen. et spec. indet. 1. **7**. Pollen in SEM. **8**. Detail of pollen surface. **9**. Pollen in LM. **10–12**. Poaceae gen. et spec. indet 3. **10**. Pollen grain in SEM. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM

**Plate 10.22** **1–3**. *Rumex* sp. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4–6**. *Persicaria* sp. 2. **4**. Pollen grain in SEM. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM. **7–9**. *Polygonum viviparum*. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view

**Plate 10.23** **1**. *Potamogeton* sp., large elliptic leaf (S 116533). **2**. *Potamogeton* sp., wide elliptic leaf (IMNH org 206). **3**. *Sorbus* aff. *aucuparia*, part of leaflet lamina (S 116537). **4**. *Sorbus* aff. *aucuparia*, elliptic leaflet (S 116537). **5**. *Sorbus* aff. *aucuparia*, detail showing marginal venation (S 116536). **6**. *Sorbus* aff. *aucuparia*, small narrow elliptic leaflet (IMNH org 217)

**Plate 10.24** **1–3**. *Thalictrum* sp. 2. **1**. Pollen grain in SEM. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM. **4–6**. *Ranunculus* sp. 1. **4**. Pollen grain in SEM. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM. **7–9**. *Ranunculus* sp. 2. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view. **10–12**. Ranunculaceae gen. et spec. indet. 2. **10**. Pollen grain in SEM, equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, equatorial view

**Plate 10.25** **1–3**. Ranunculaceae gen. et spec. indet. 4. **1**. Pollen grain in SEM, oblique view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, polar view. **4–6**. Ranunculaceae gen. et spec. indet. 5. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7–9**. *Filipendula* sp. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view. **10–12**. *Fragaria* sp. 1. **10**. Pollen grain in SEM, equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, equatorial view

**Plate 10.26** **1**. *Salix gruberi*, wide elliptic leaf (IMNH org 214). **2**. *Salix gruberi*, upper part of leaf (IMNH org 223). **3**. *Salix gruberi*, part of leaf (S 116542). **4**. *Salix* sp. B (*S. arctica* type). **5**. Seeds, unnasigned

**Plate 10.27** **1–3**. *Rubus* sp. **1**. Pollen in SEM, equatorial view. **2**. Detail of pollen surface. **3**. Pollen grain in LM, equatorial view. **4–6**. *Sanguisorba* sp. **4**. Pollen grain in polar view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, polar view. **7–9**. Rosaceae gen. et spec. indet. 11. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view. **10–12**. *Potentilla* sp. 1. **10**. Pollen grain in SEM, equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, equatorial view

**Plate 10.28** **1–3**. *Salix* sp. 5. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4–6**. *Salix* sp. 4. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7–9**. *Acer* sp. l. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view. **10–12**. *Acer* sp. 2. **10**. Pollen grain in SEM, equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, equatorial view

**Plate 10.29** **1–3**. *Sparganium* sp. **1**. Pollen grain in SEM. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM. **4–6**. *Tetracentron atlanticum*. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7–9**. aff. *Valeriana* sp. **7**. Pollen grain in SEM, oblique view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, oblique view. **10–12**. *Viscum* aff. *album*. 1. Pollen in SEM. **11**. Detail of pollen grain surface. **12**. Pollen in LM

**Plate 10.30** **1–3**. Monocotyledonae fam. gen. et spec. indet 1. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface close to sulcus. **3**. Pollen grain in LM. **4–6**. Pollen type 24. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen surface. **6**. Pollen grain in LM, equatorial view. **7–9**. Pollen type 24. **7**. Pollen grain in SEM, oblique equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen in LM, equatorial view. **10–12**. Pollen type 25. **10**. Pollen in SEM, equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen in LM, equatorial view. **13–15**. Pollen type 26. **13**. Pollen in SEM, equatorial view. **14**. Detail of pollen grain surface. **15**. Pollen grain in LM, equatorial view

**Plate 10.31** **1–3**. Pollen type 27. **1**. Pollen grain in SEM. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM. **4–6**. Pollen type 27. **4**. Pollen grain in SEM. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM. **7–9**. Pollen type 29. **7**. Pollen grain in SEM. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM. **10–12**. Pollen type 30. **10**. Pollen in SEM. **11**. Detail of pollen surface. **12**. Pollen in LM

# Plates

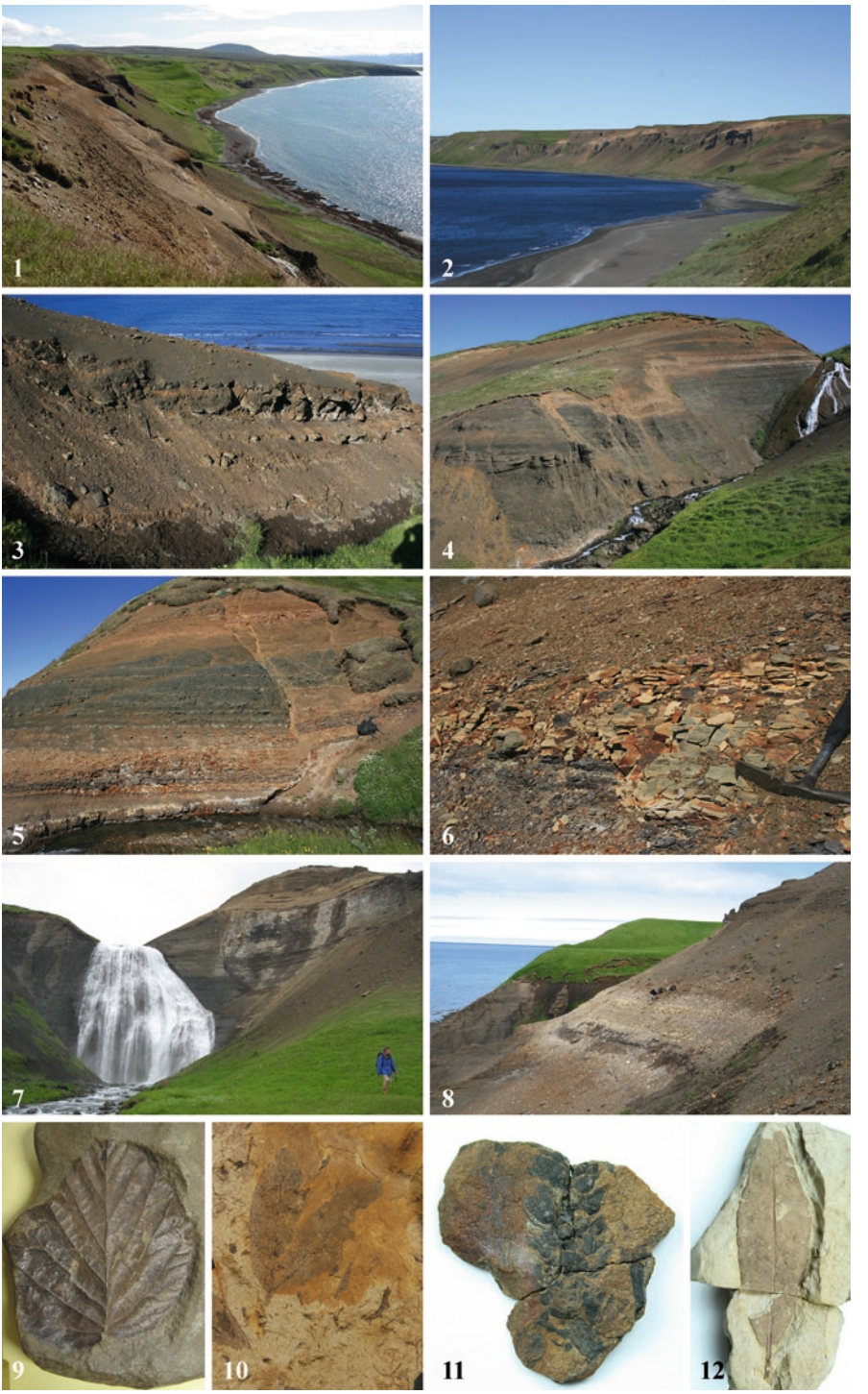



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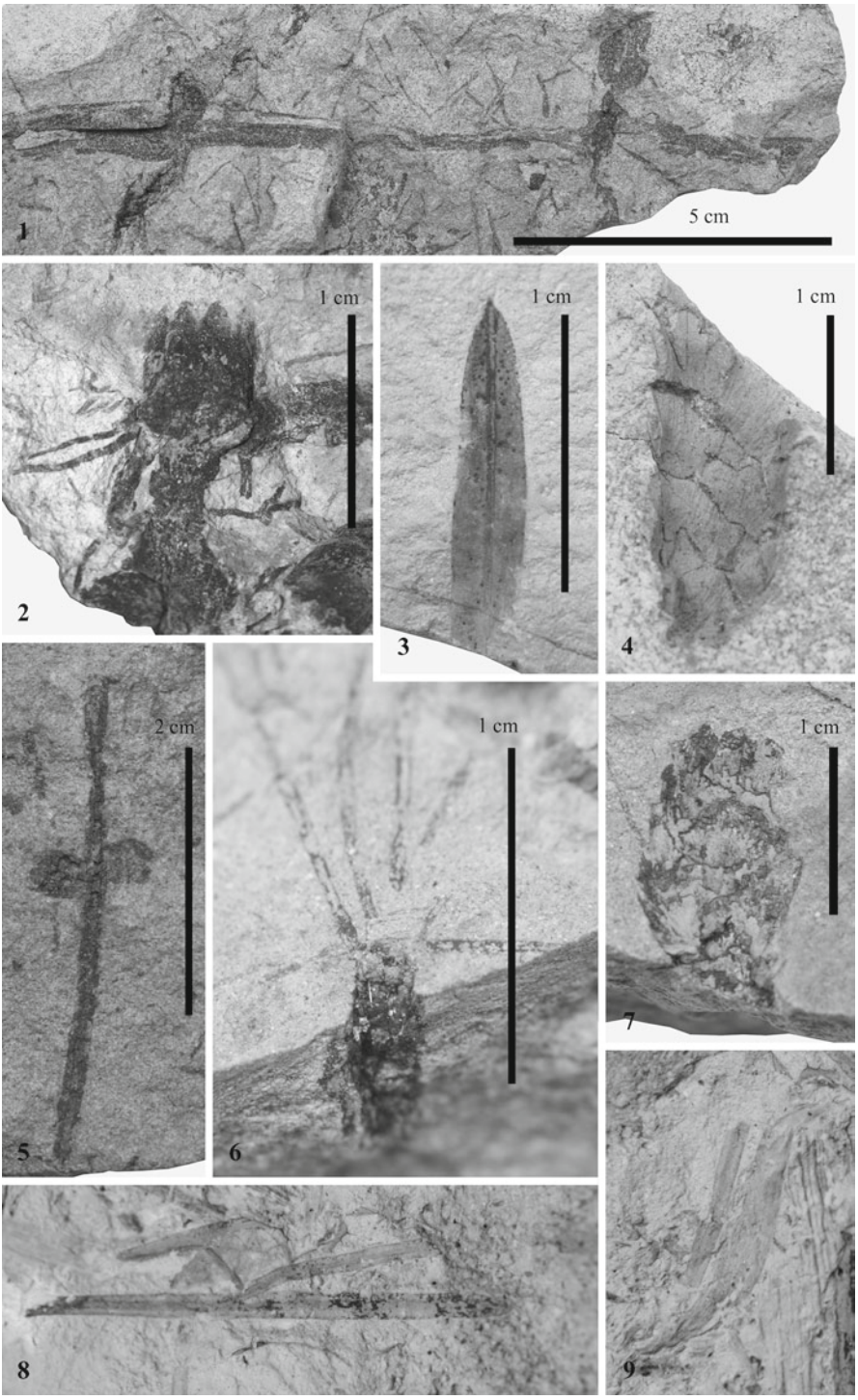



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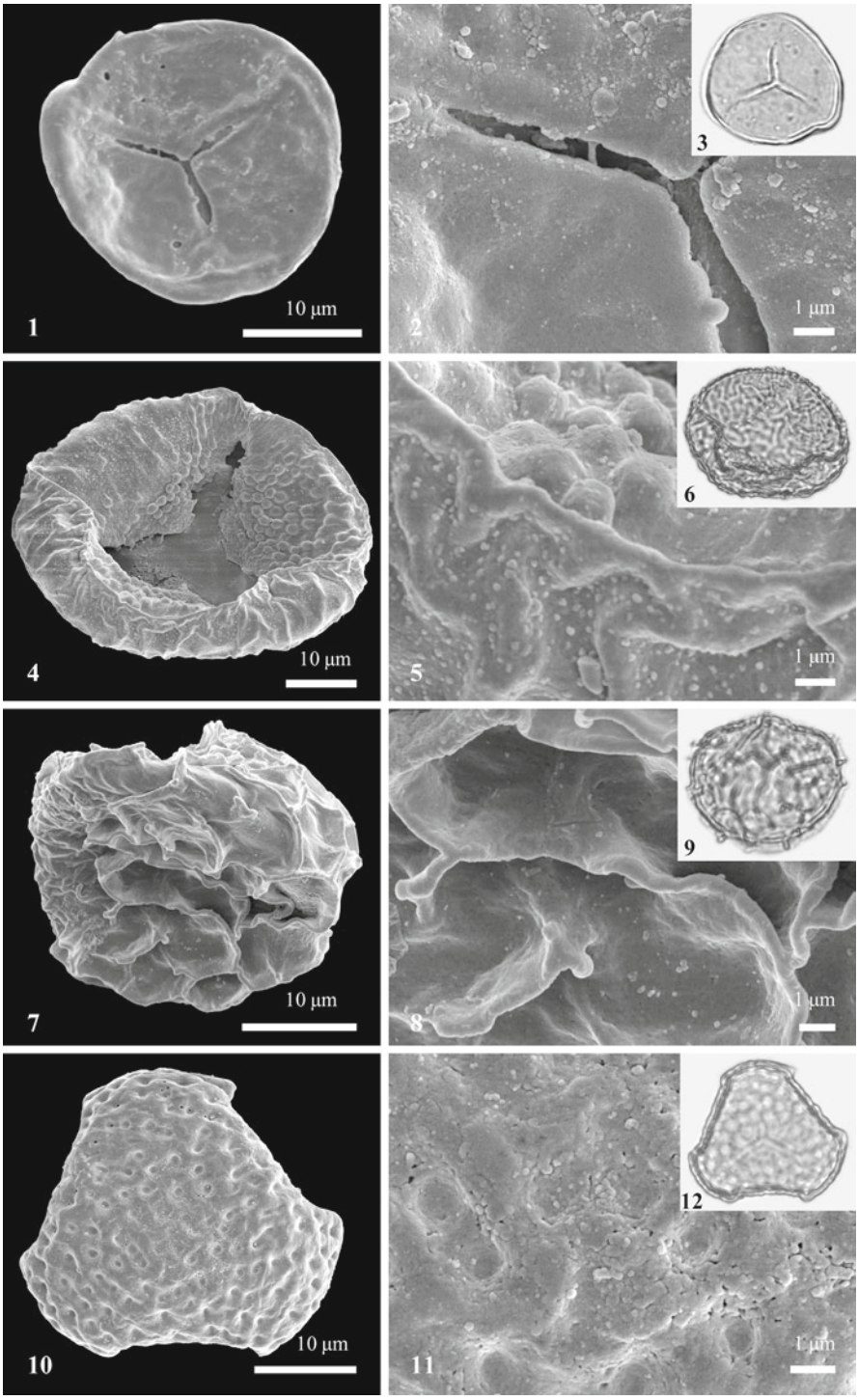



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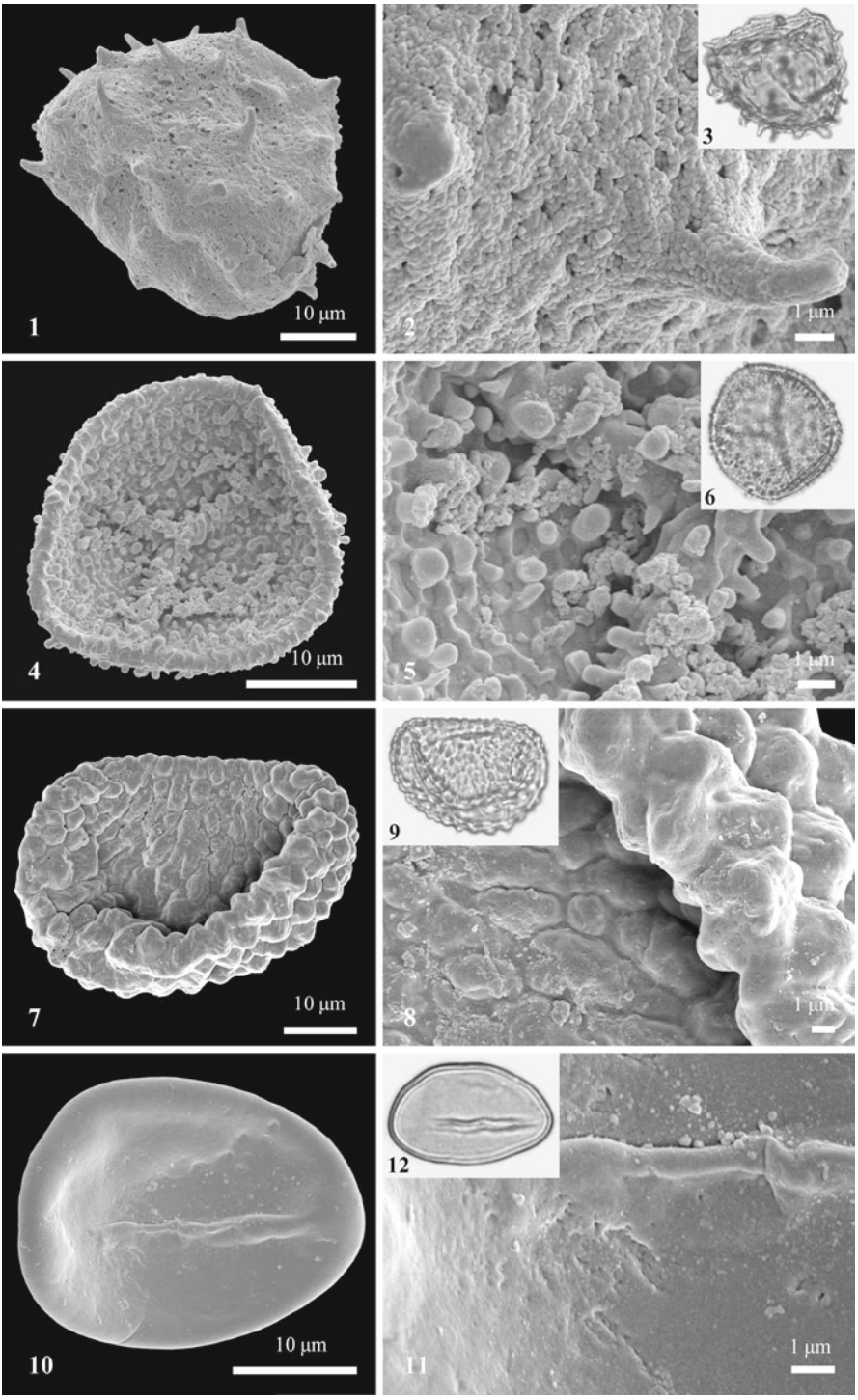



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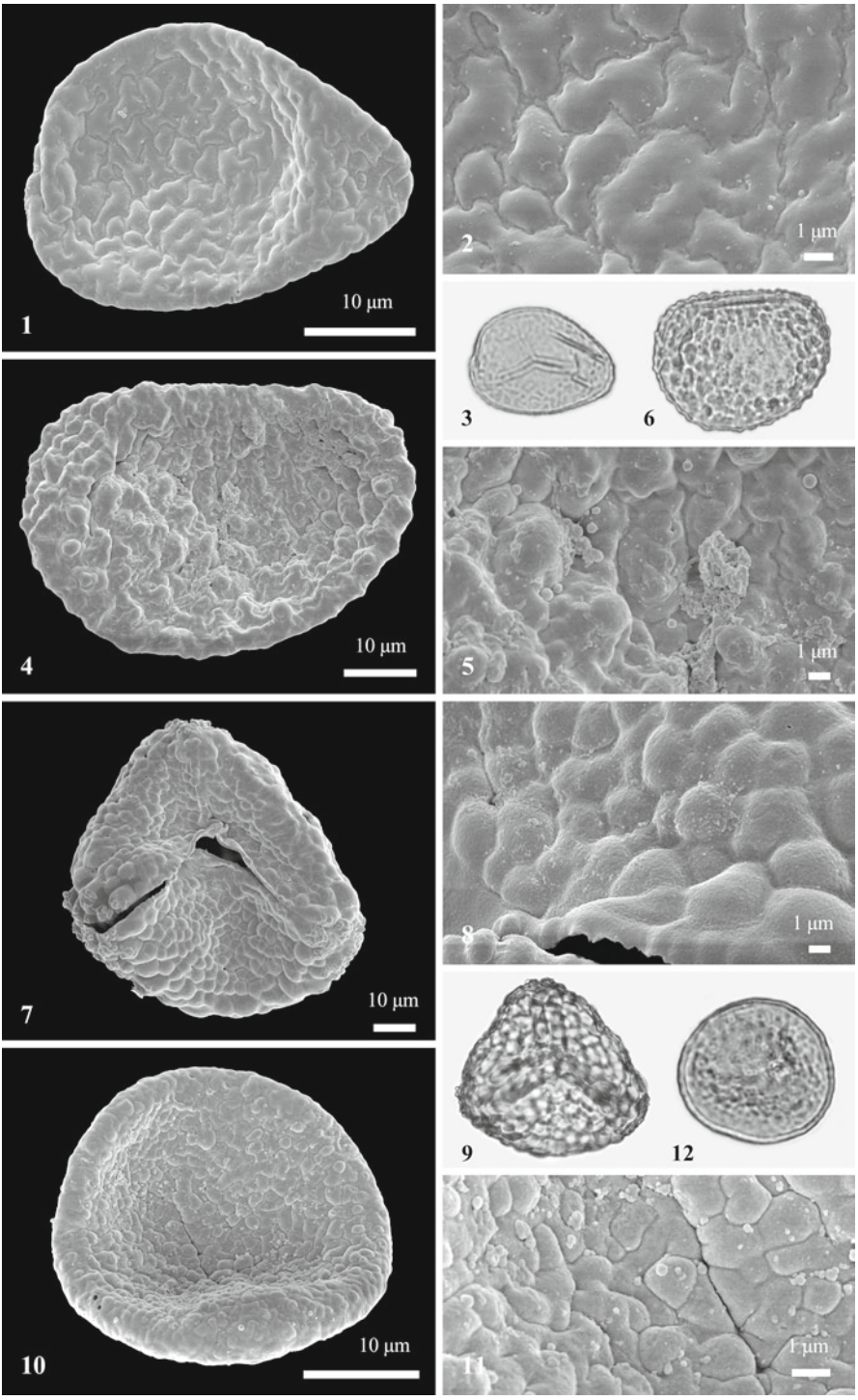



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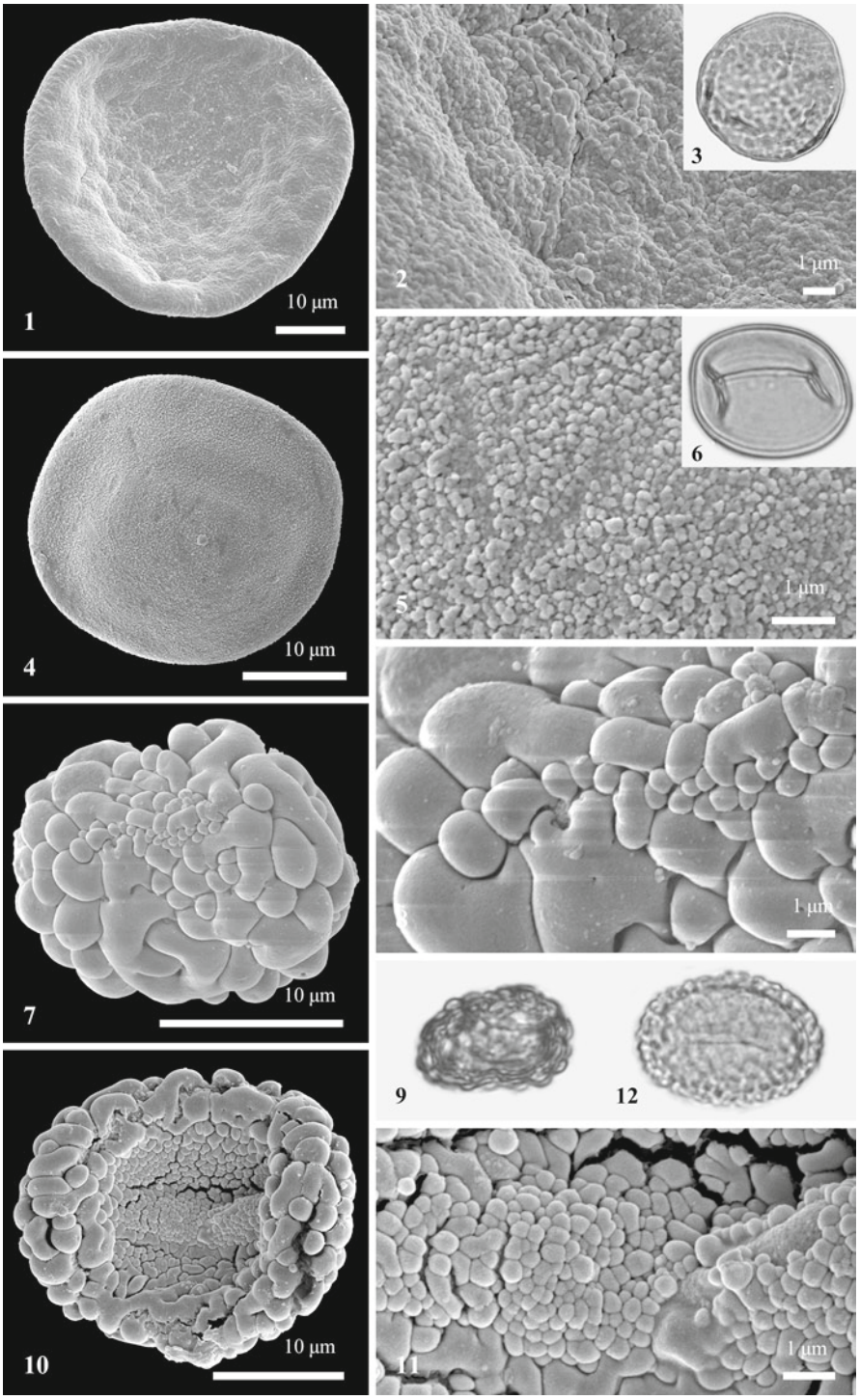



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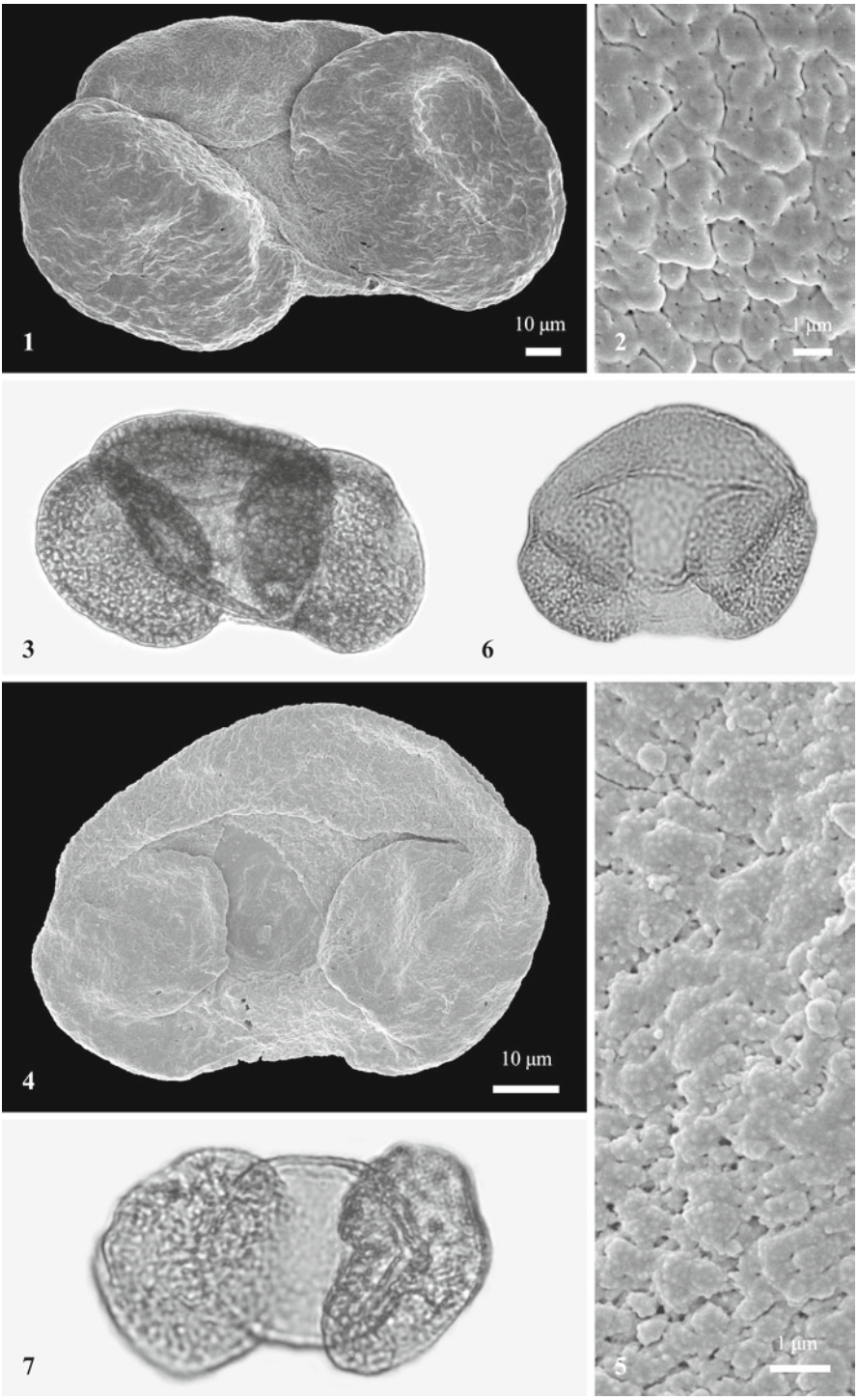



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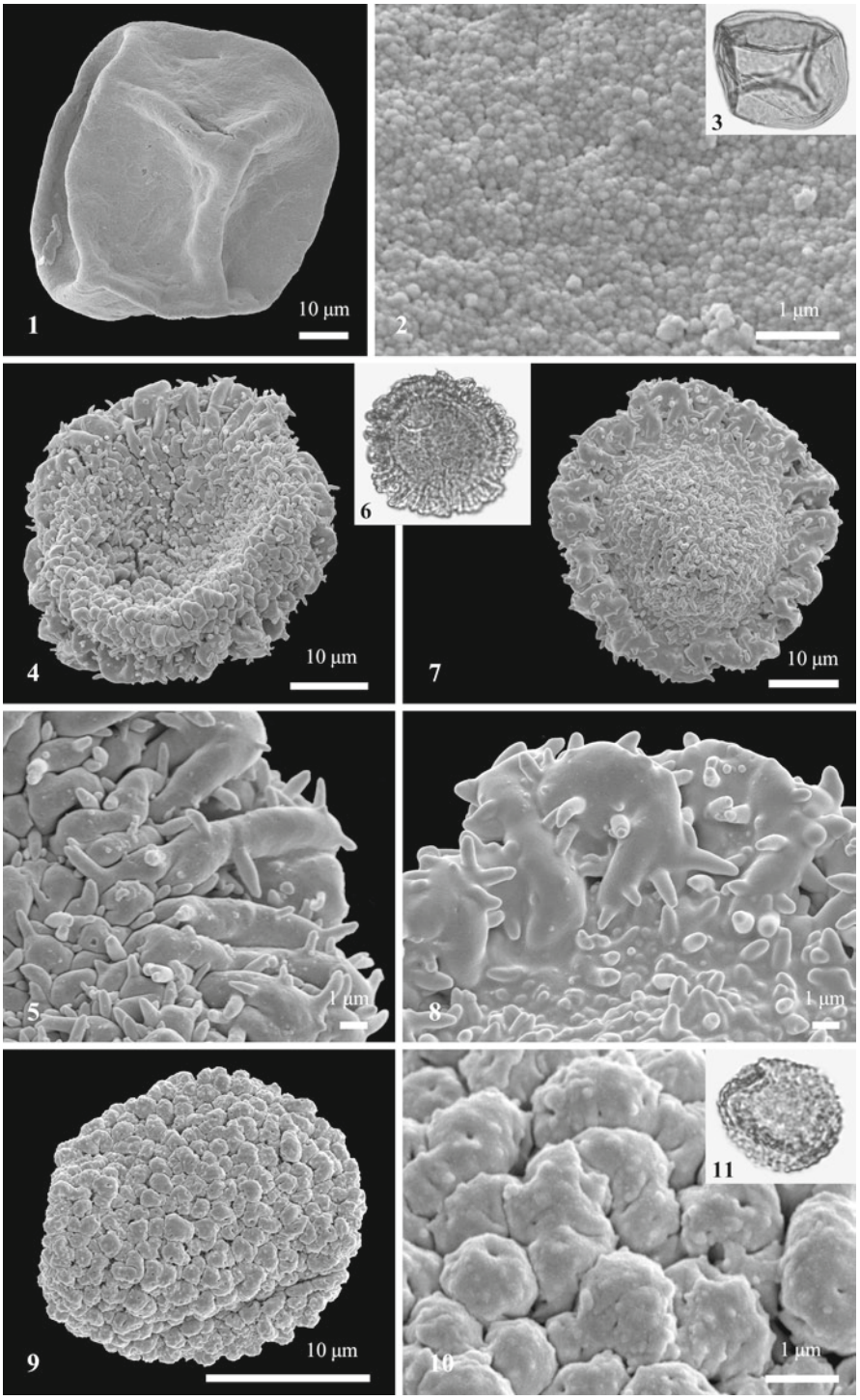



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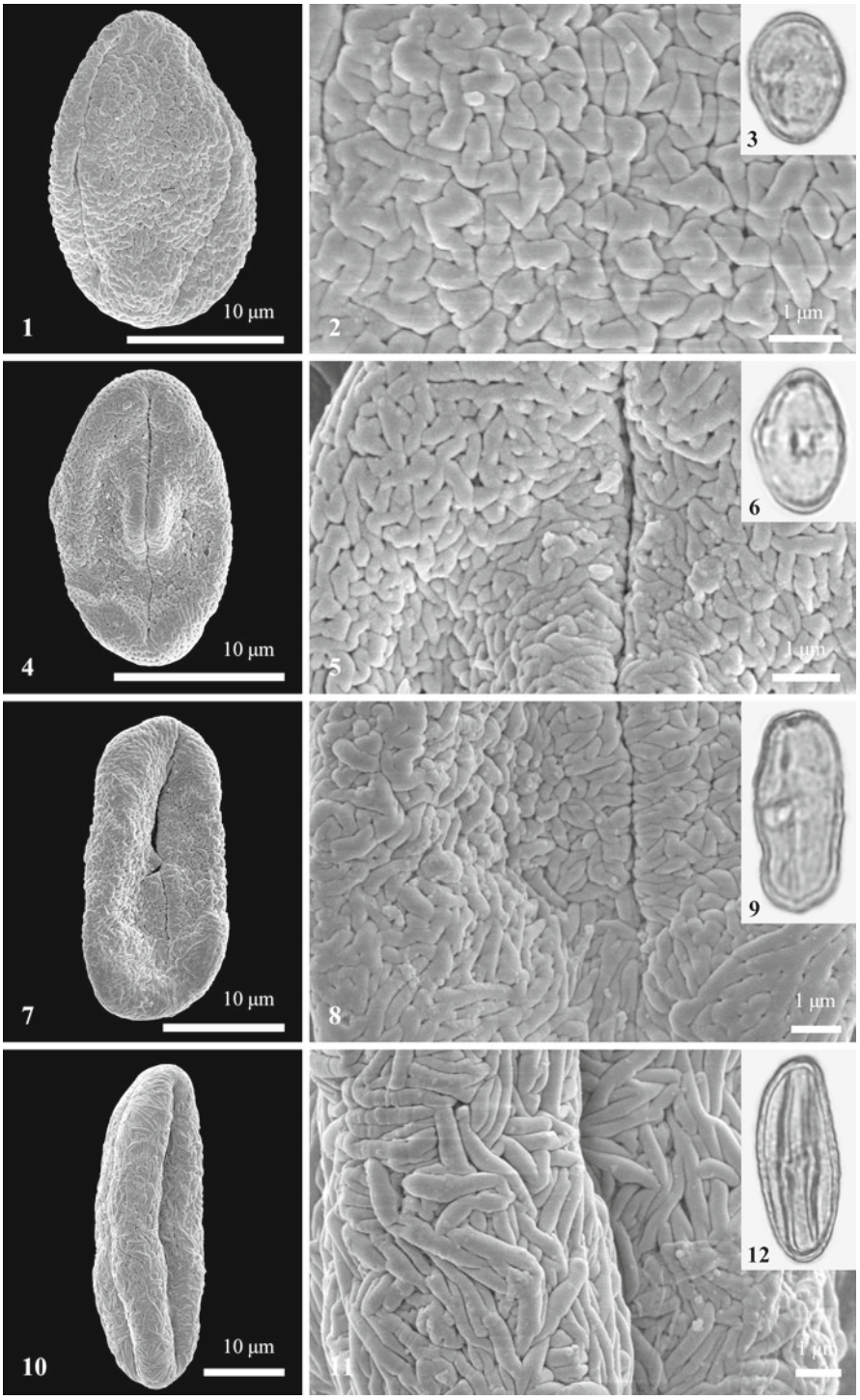



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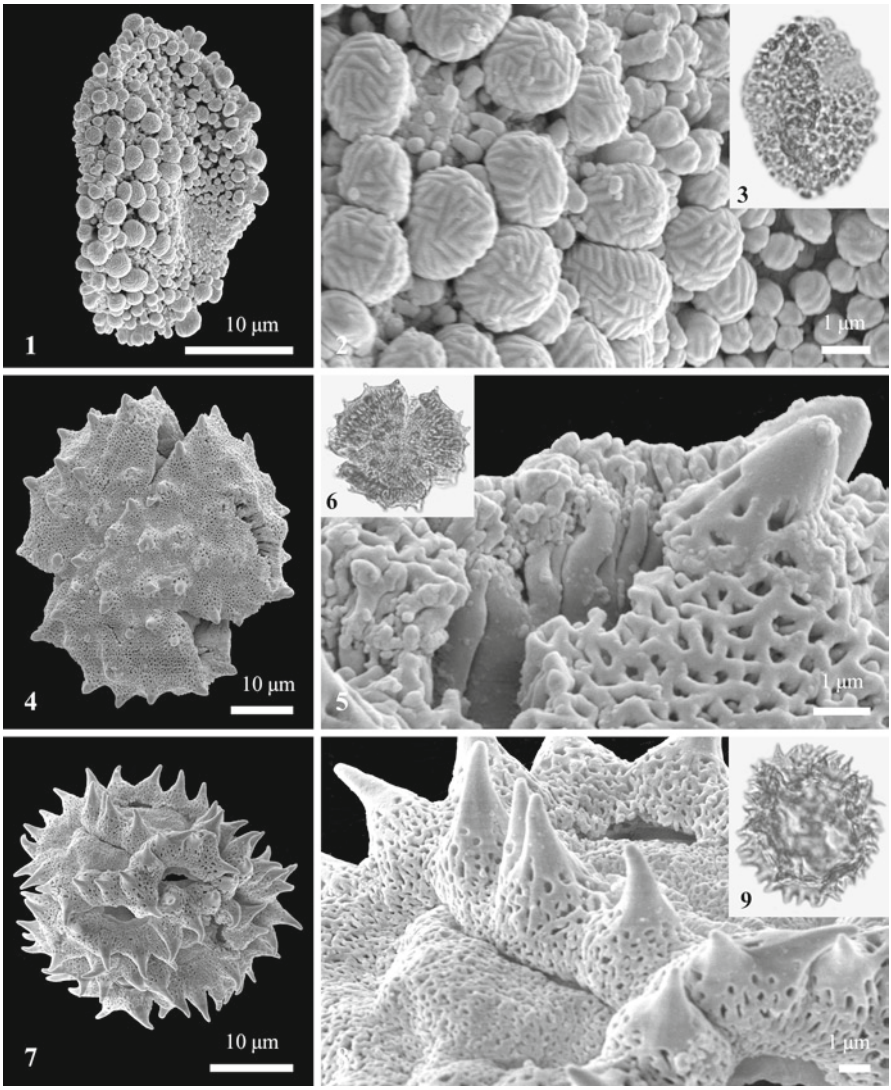



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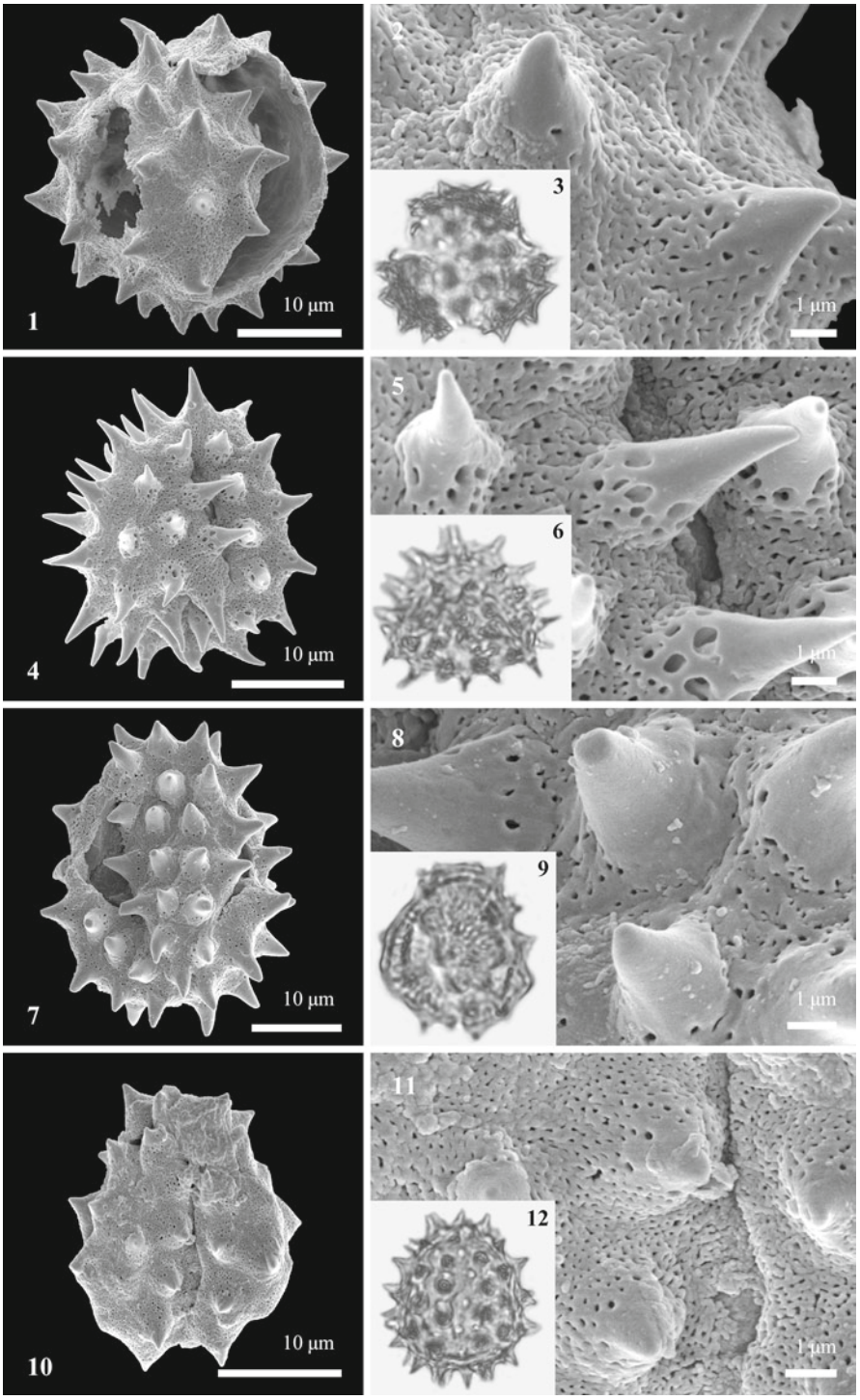



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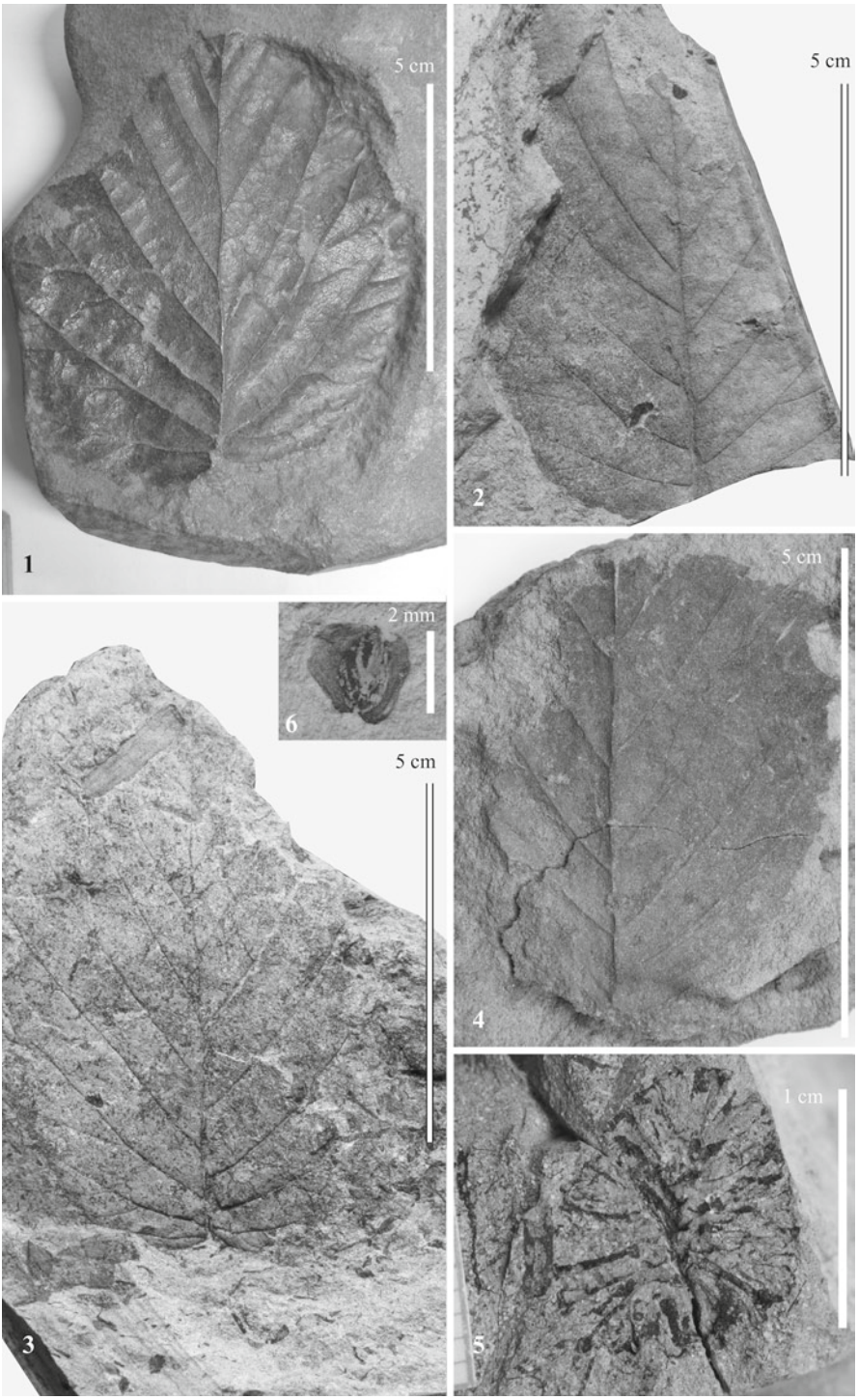



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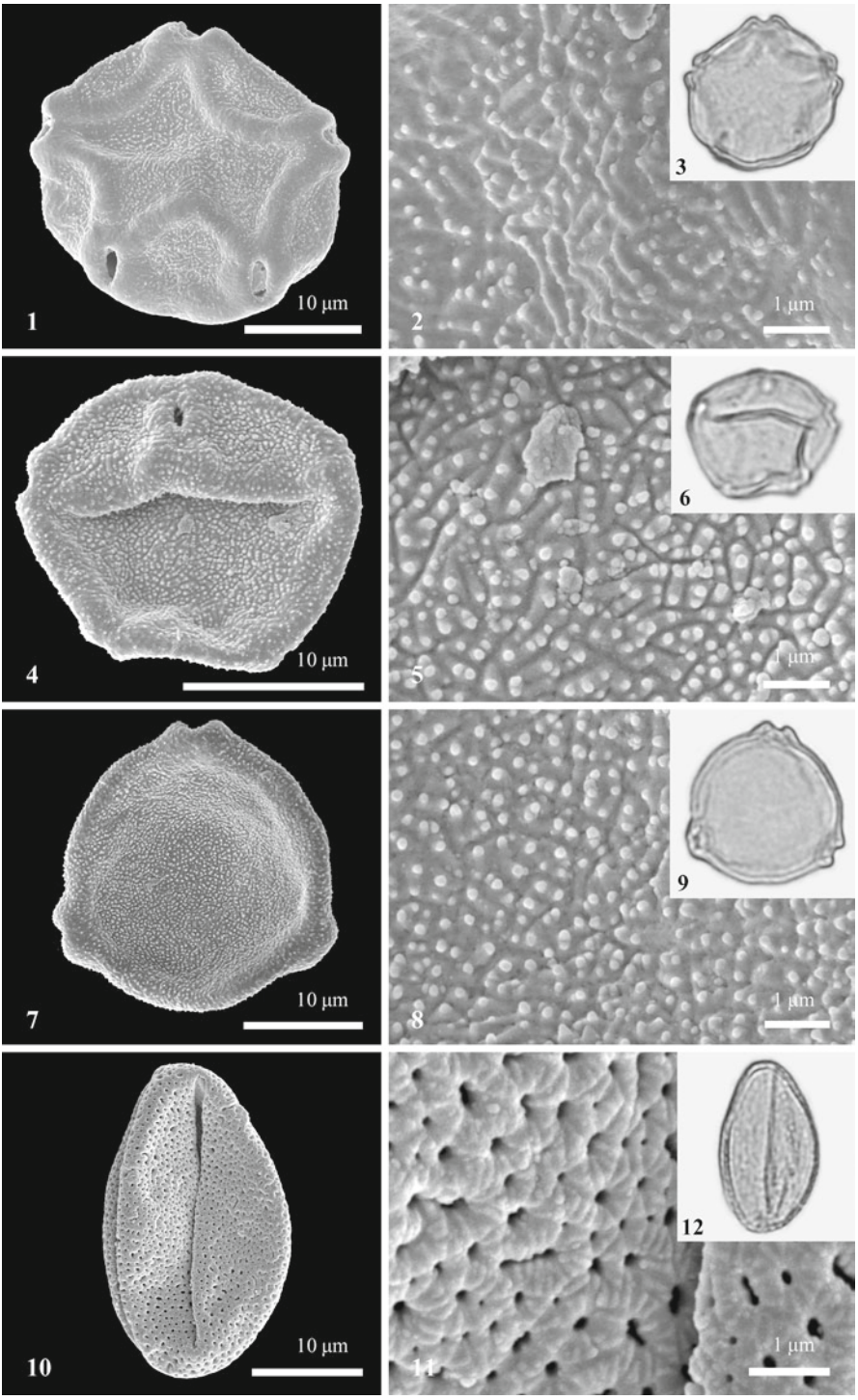



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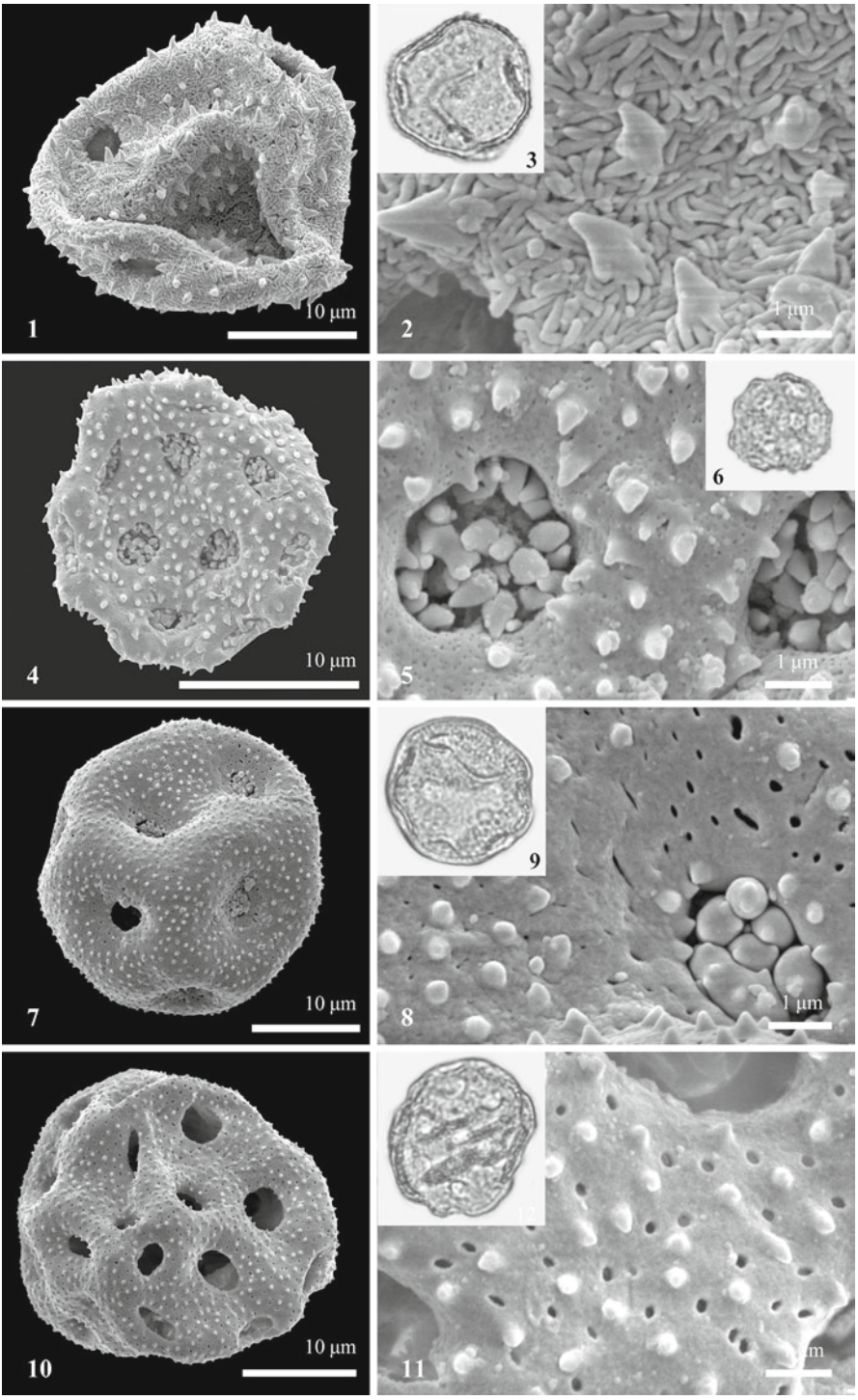



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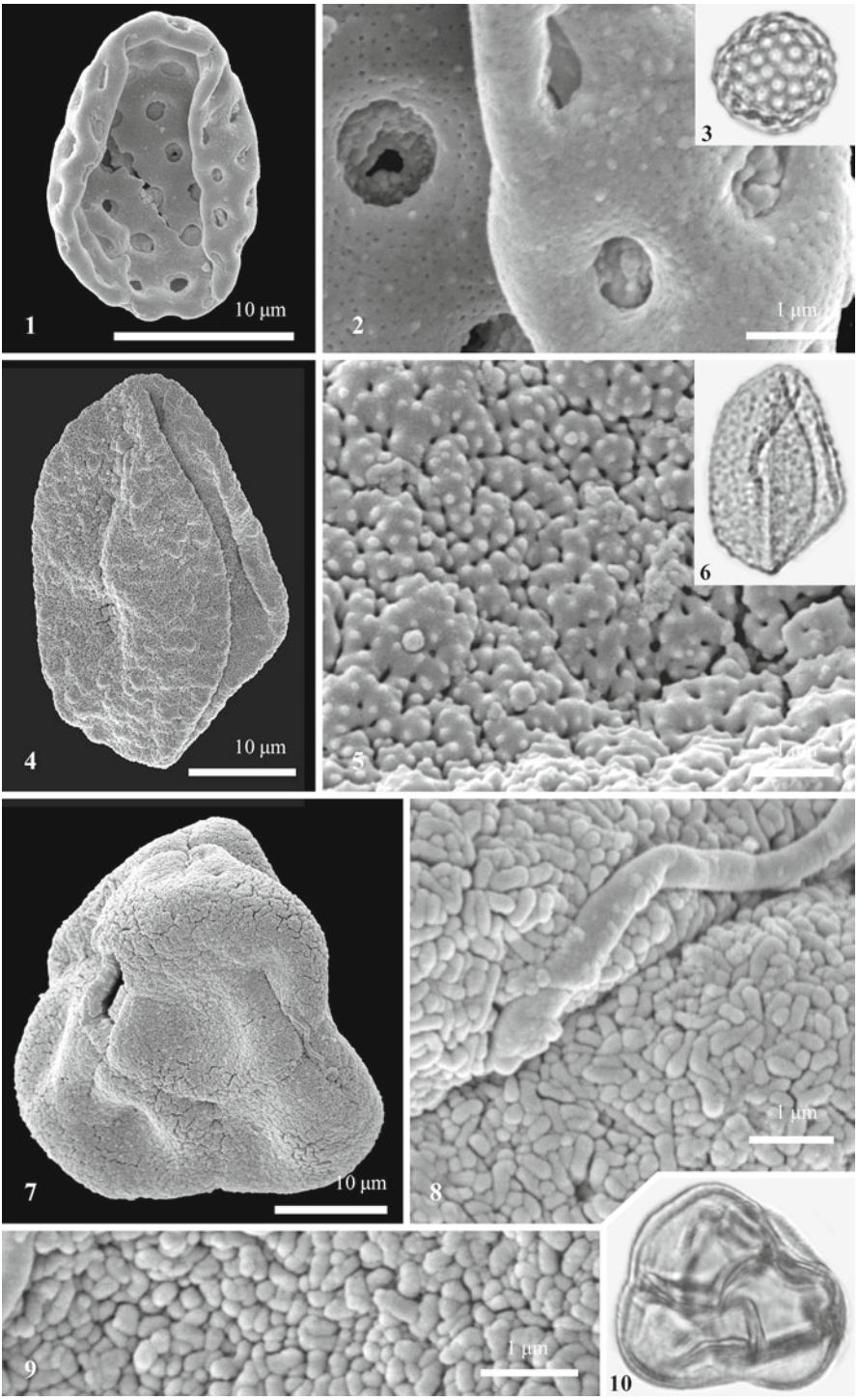



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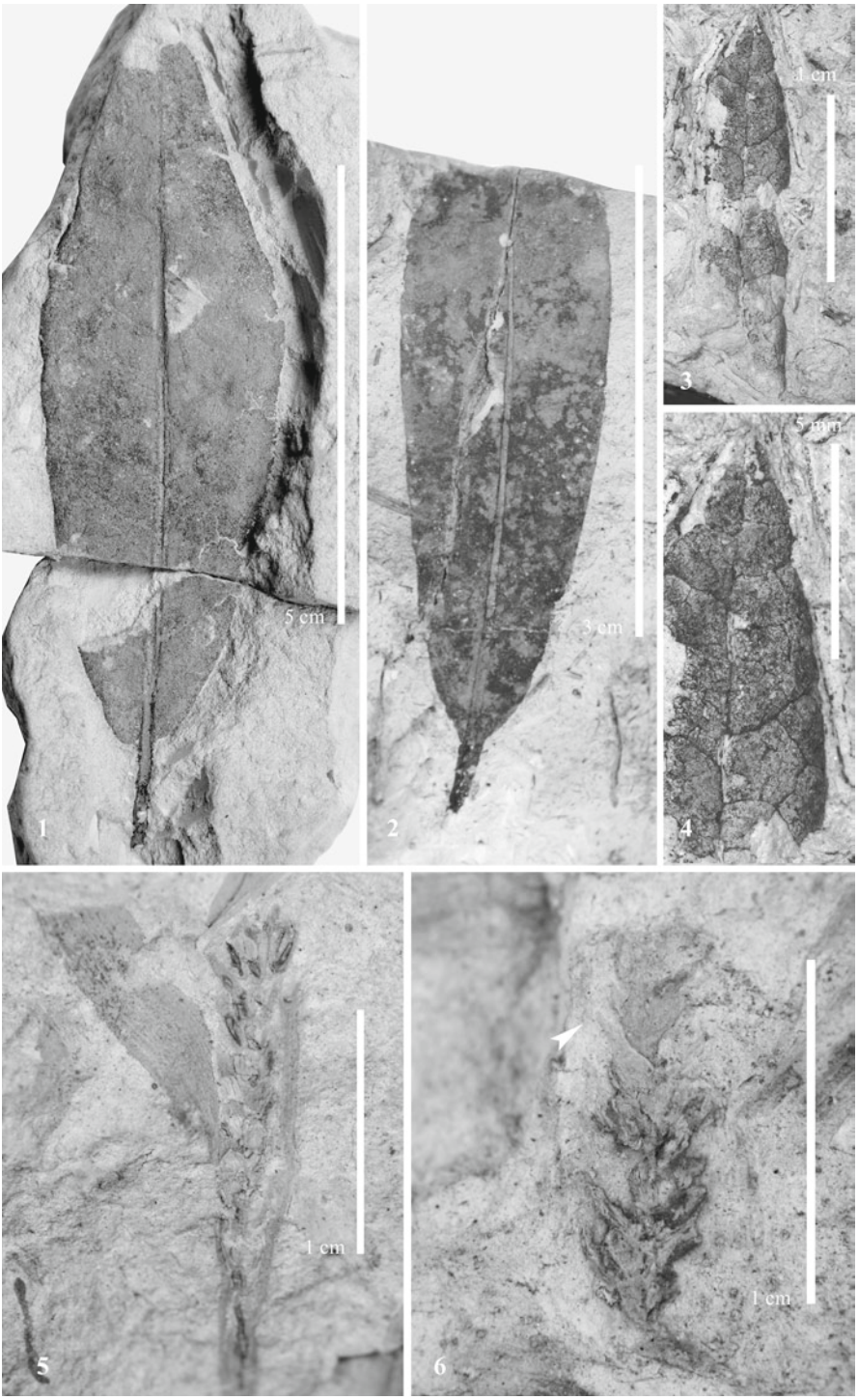



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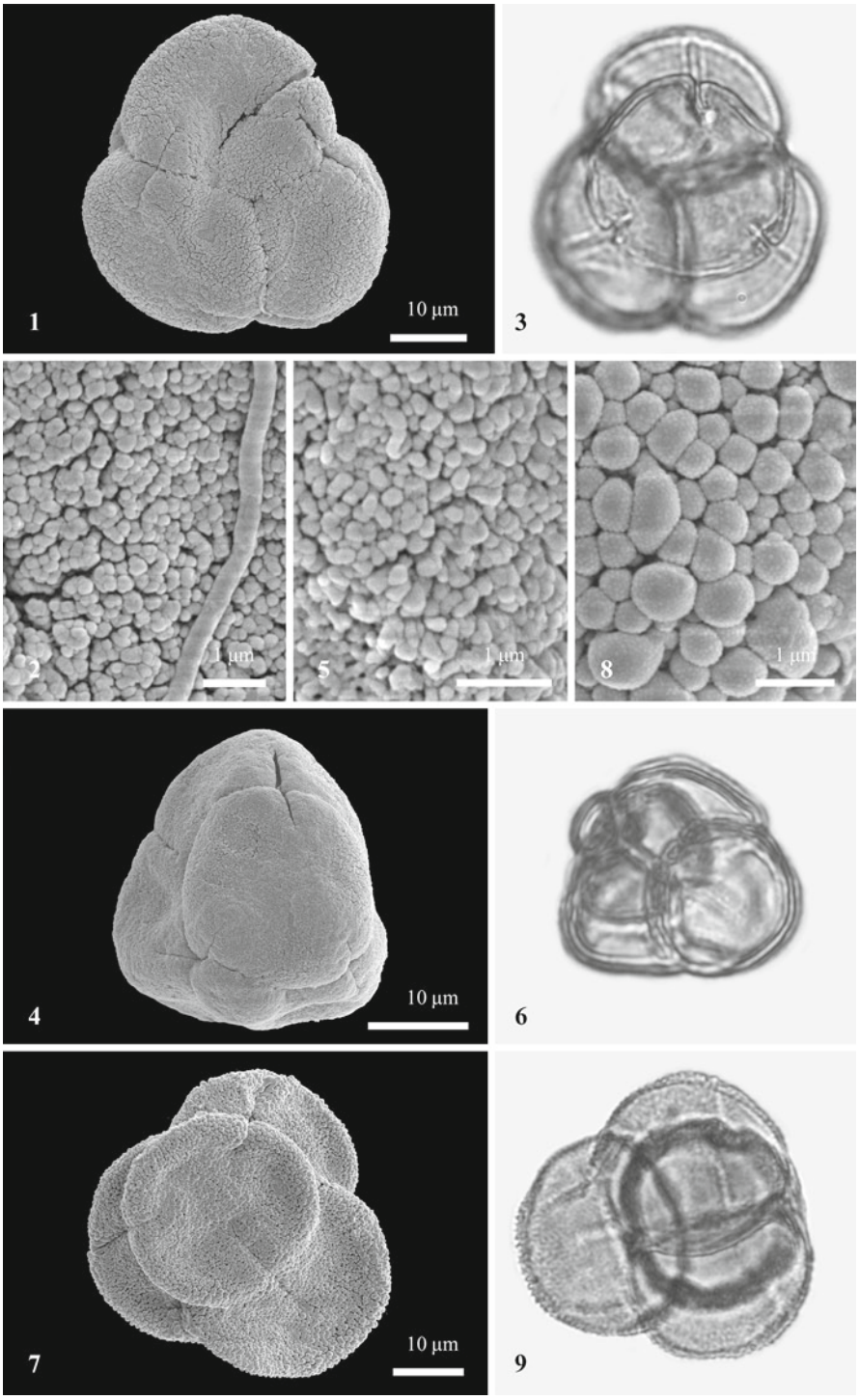



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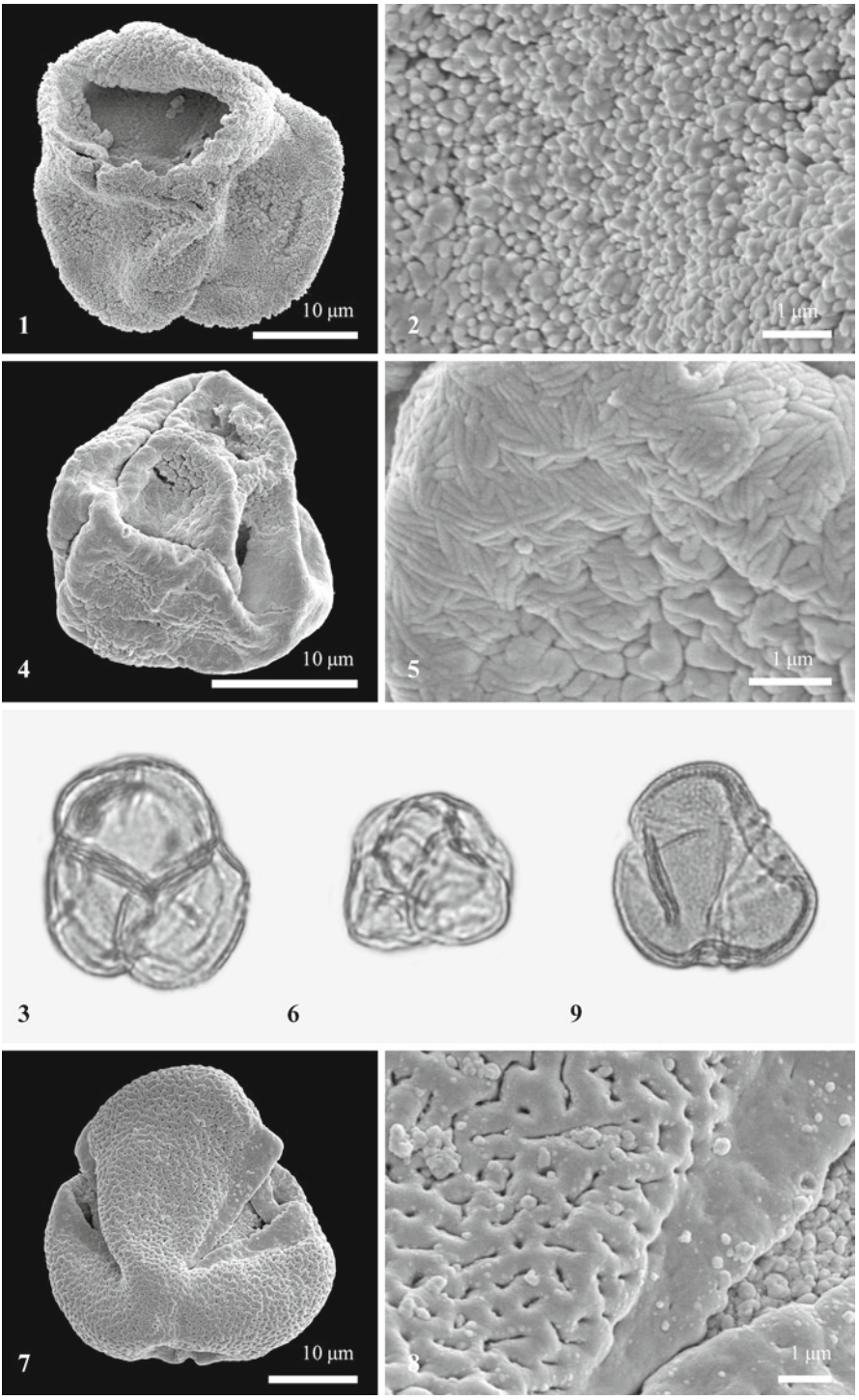



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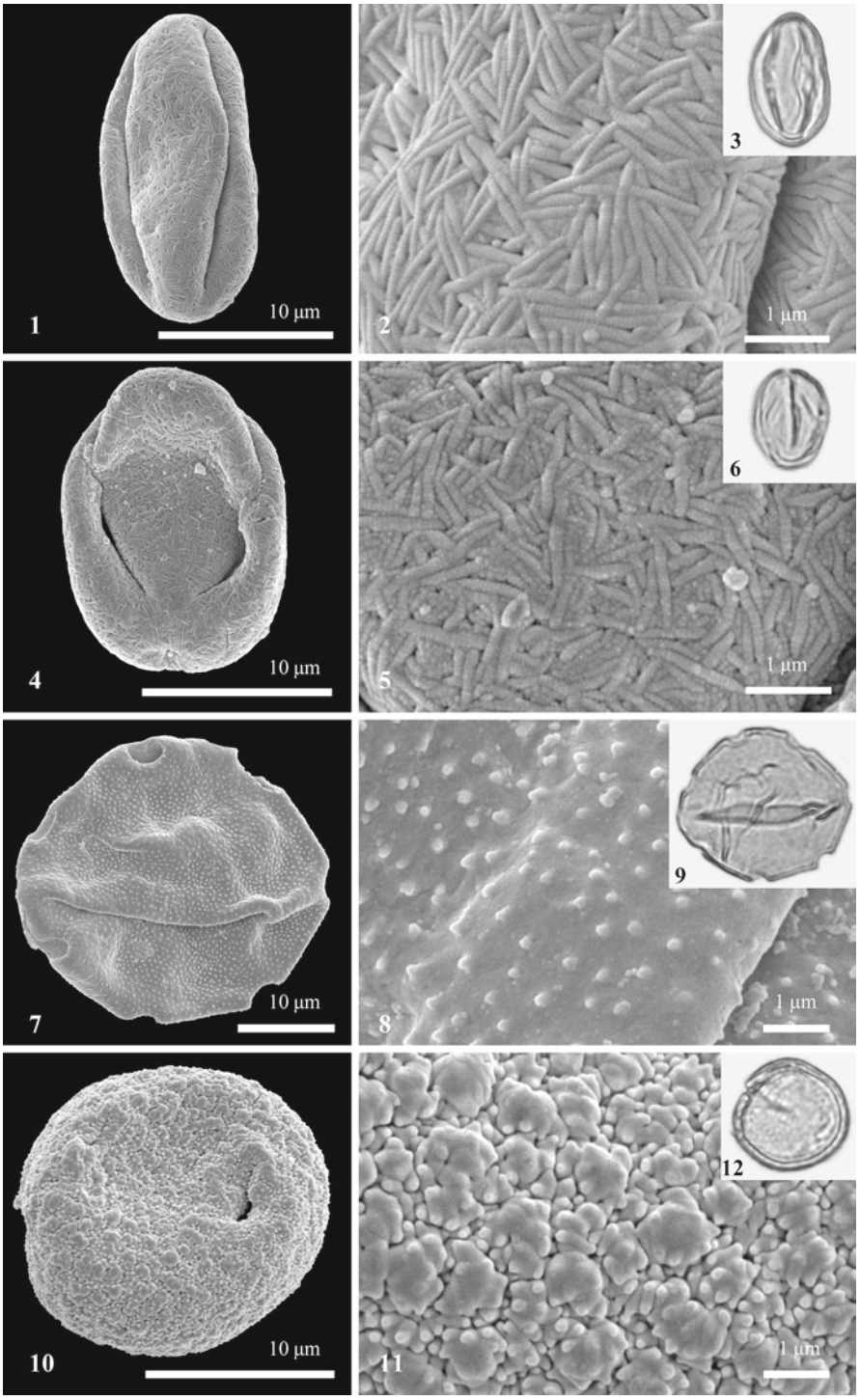



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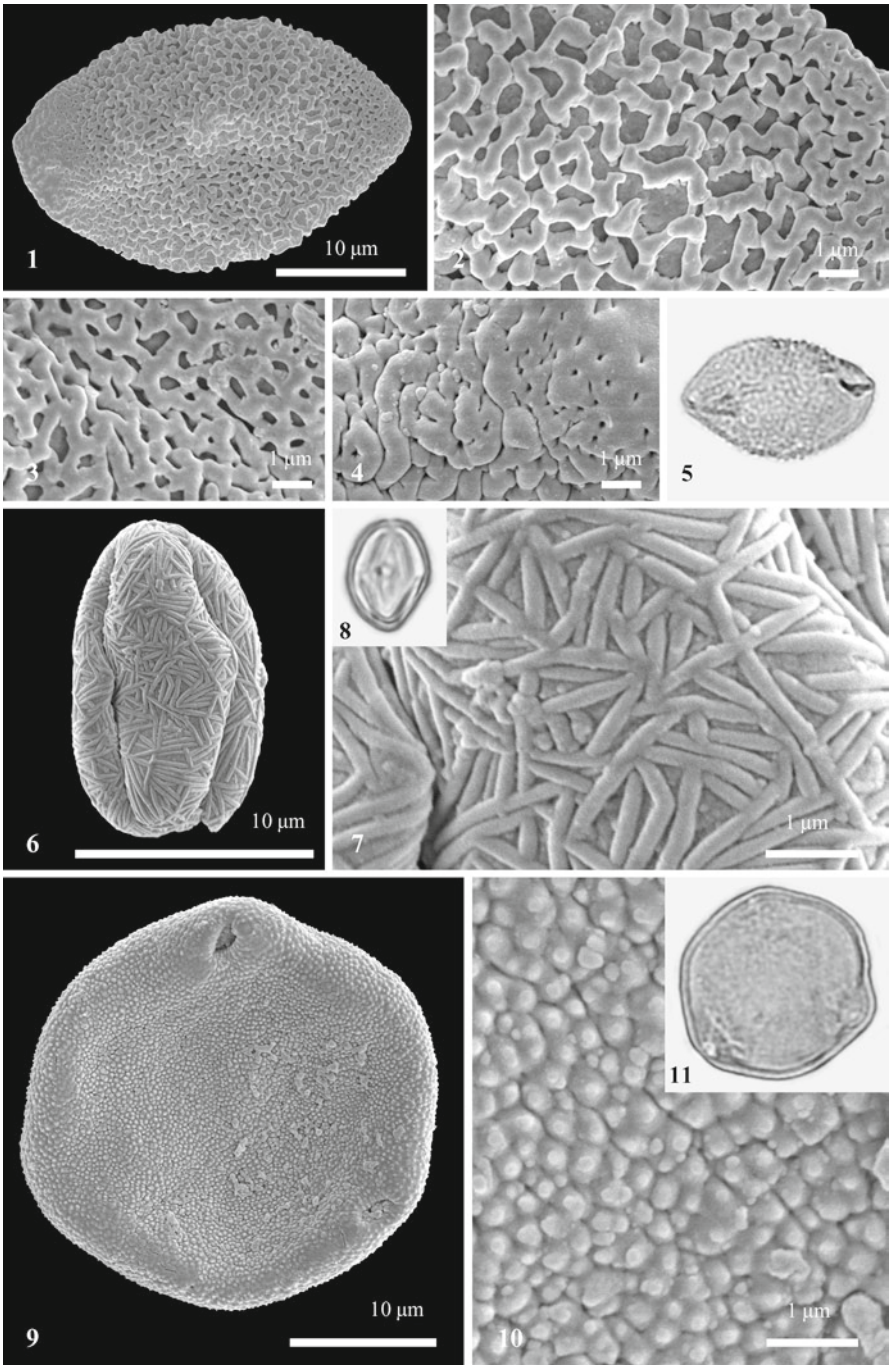



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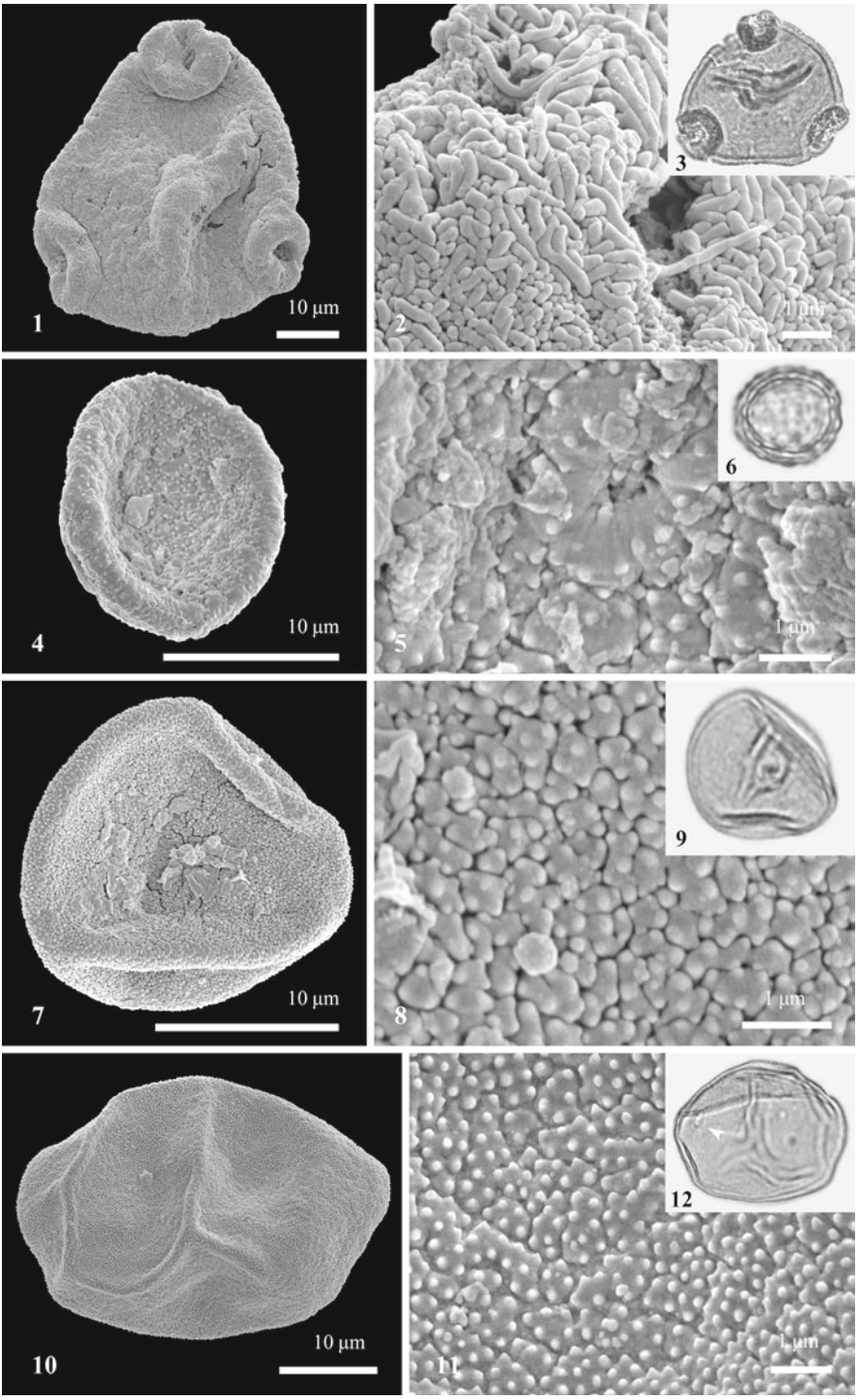



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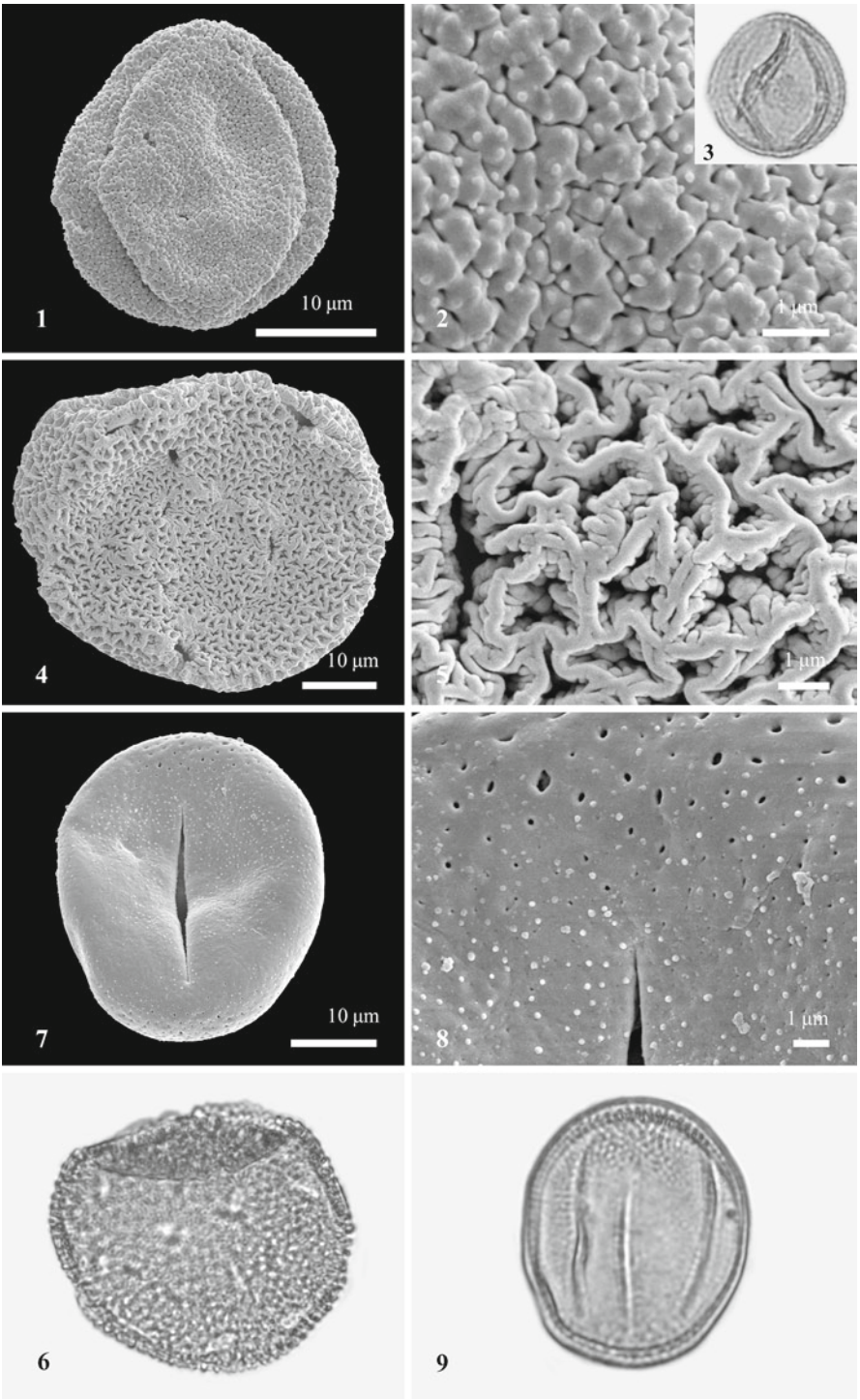



**Plate 10.22**

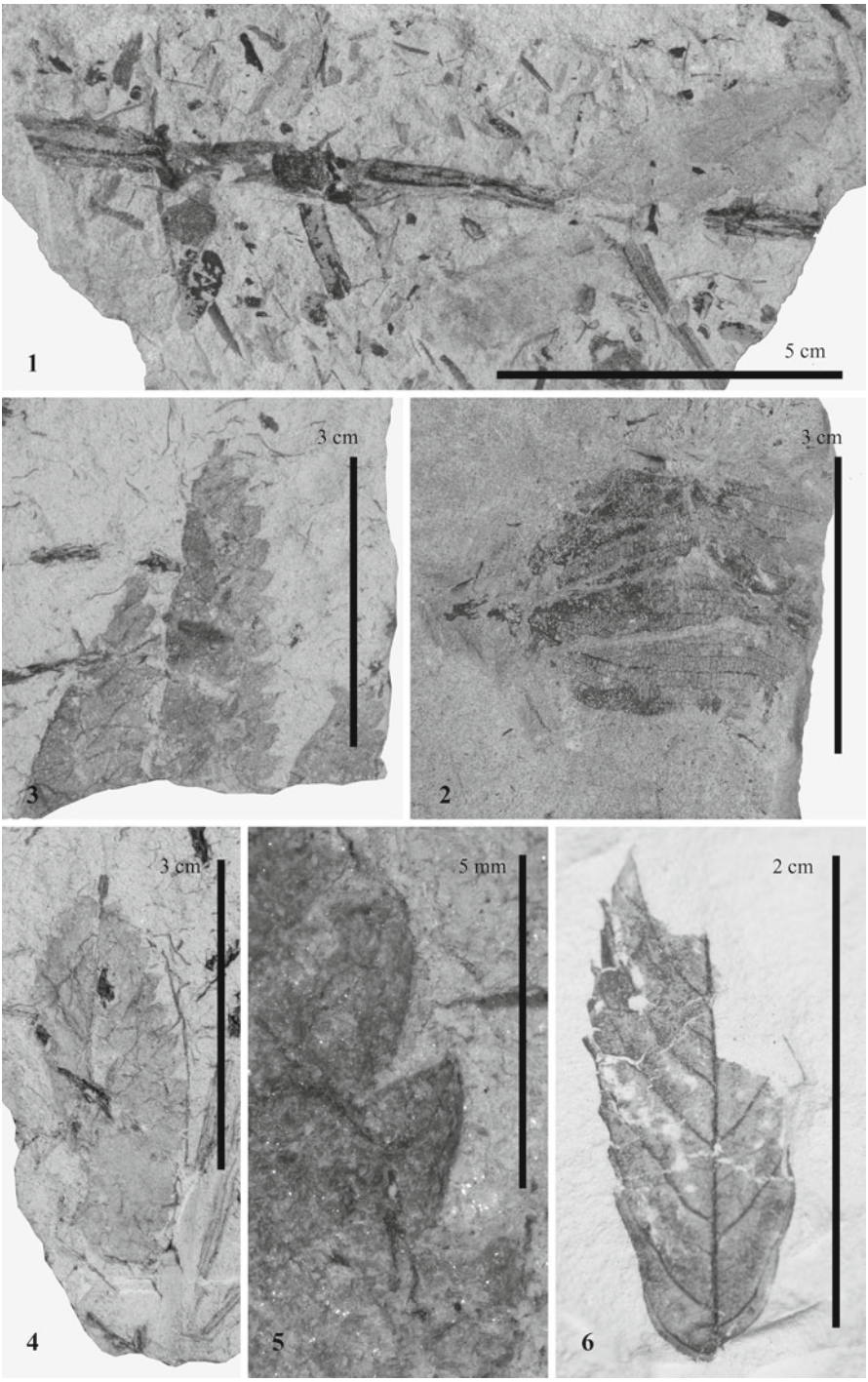



**Plate 10.23**

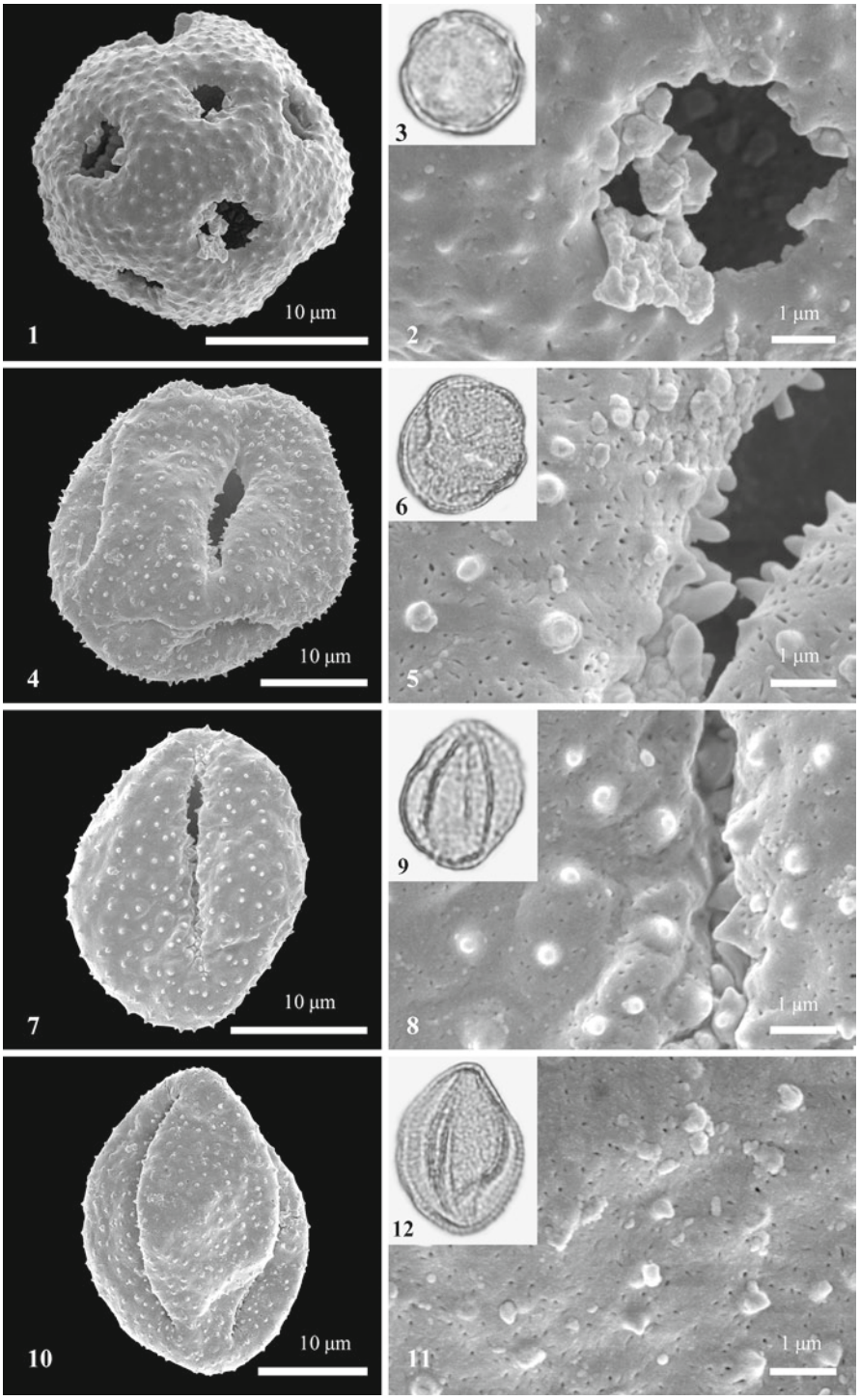



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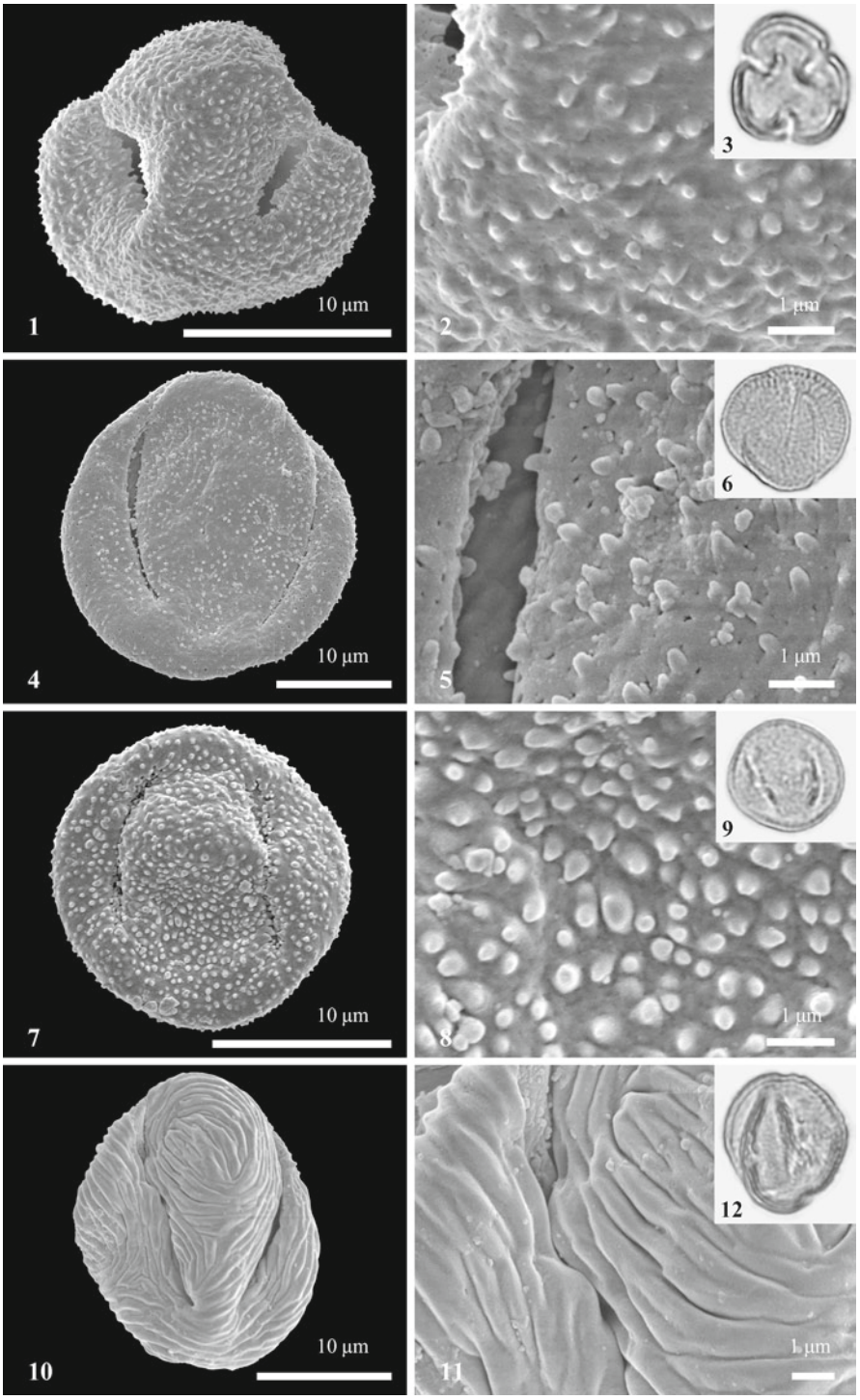



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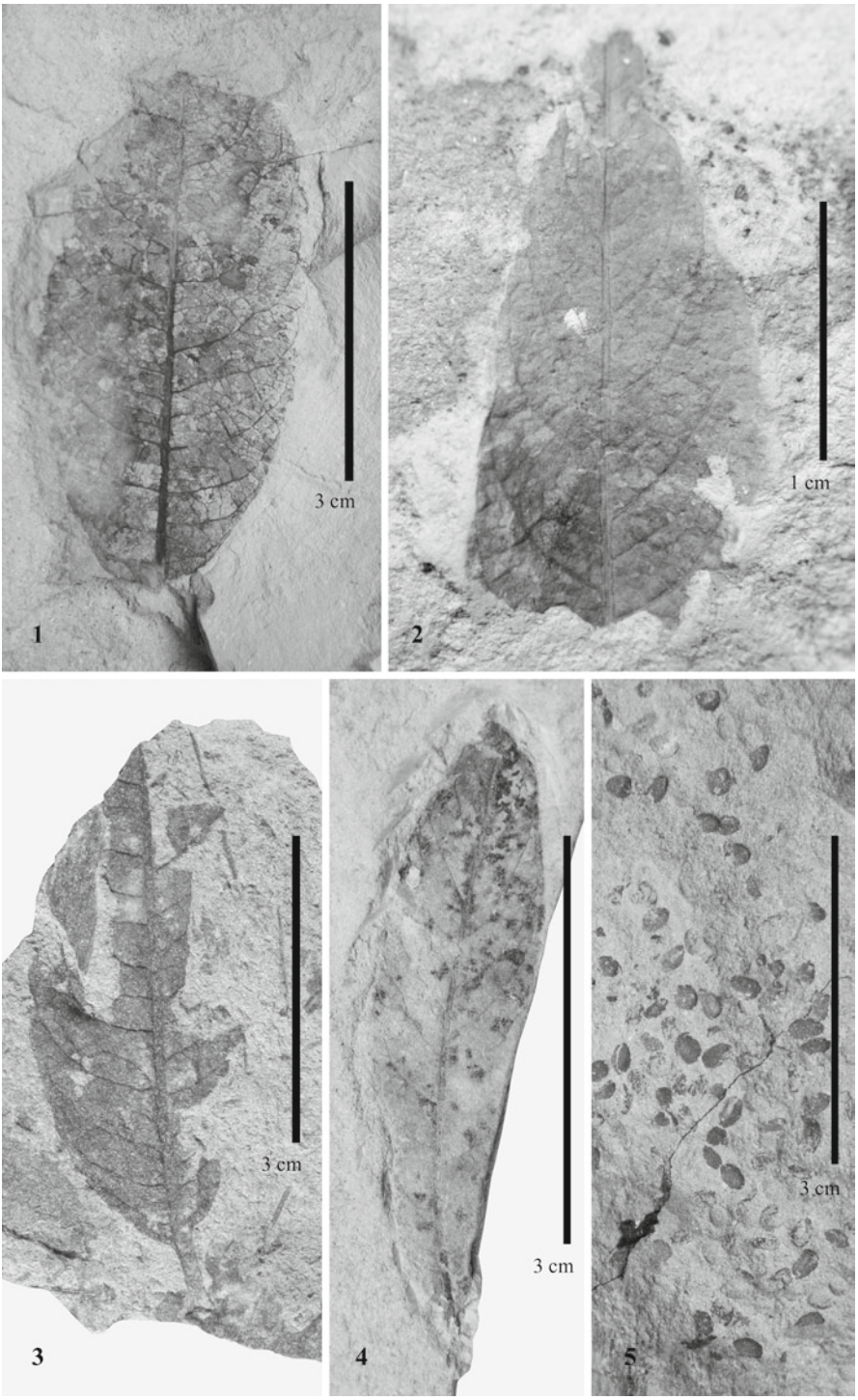



**Plate 10.26**

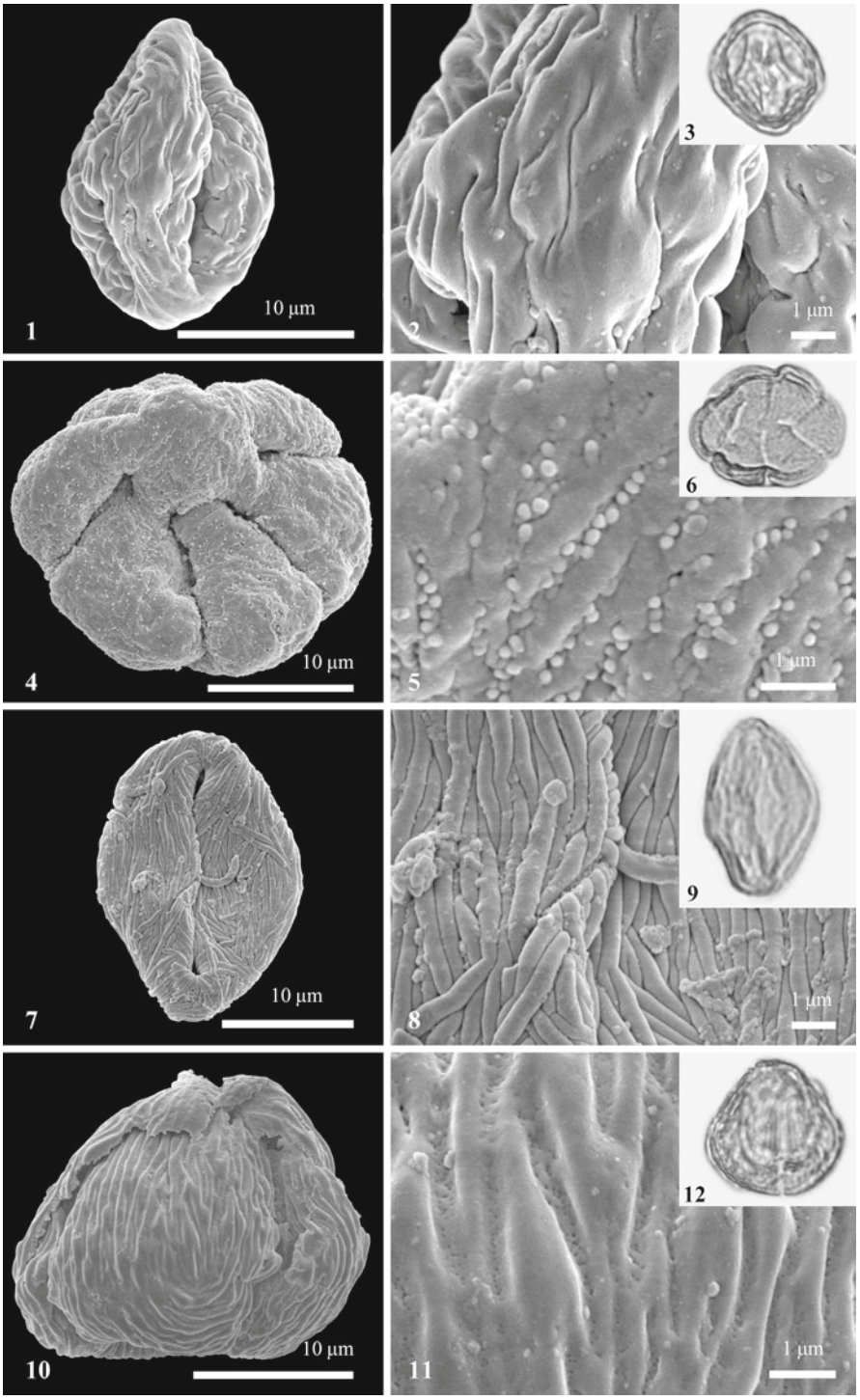



**Plate 10.27**

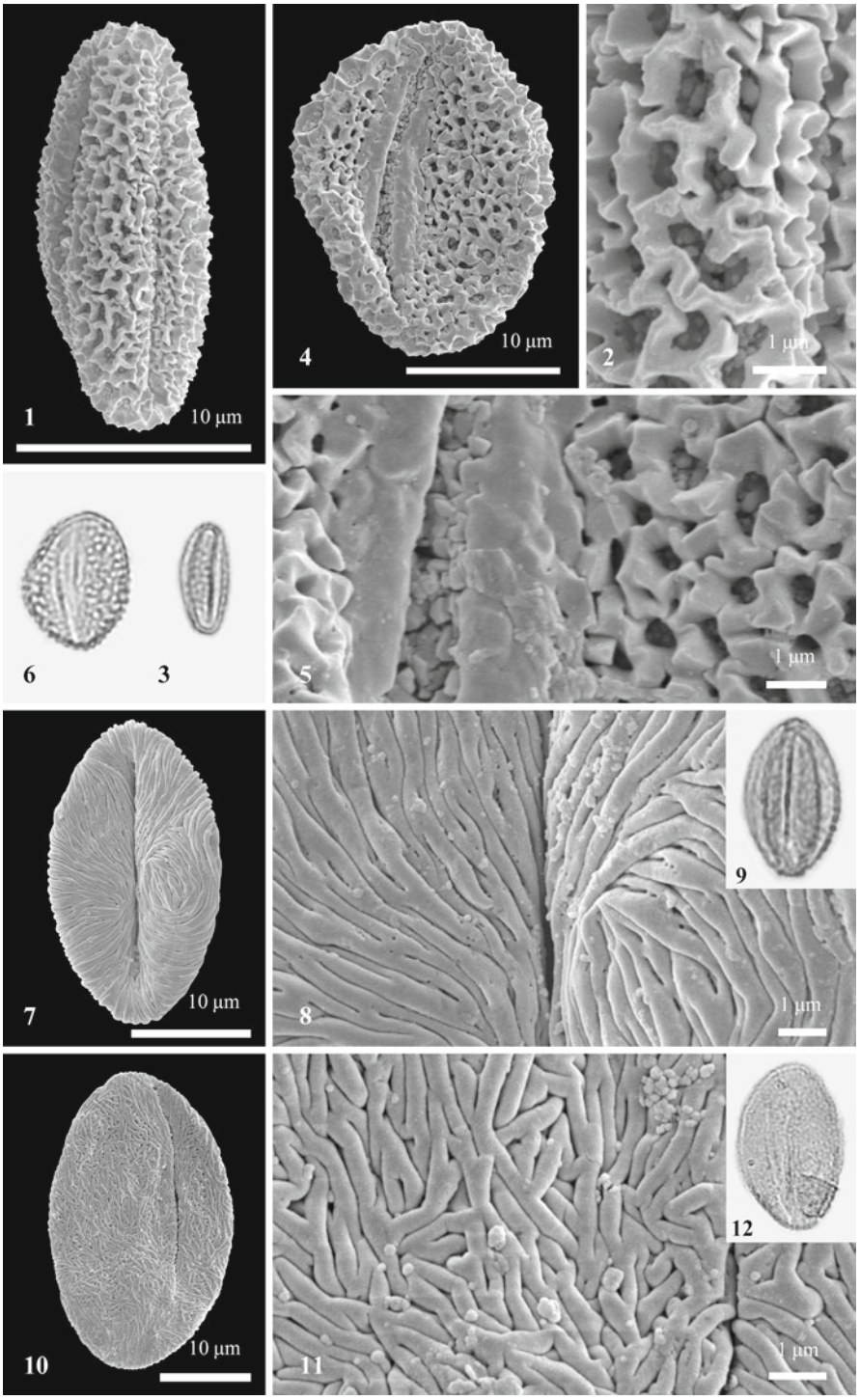



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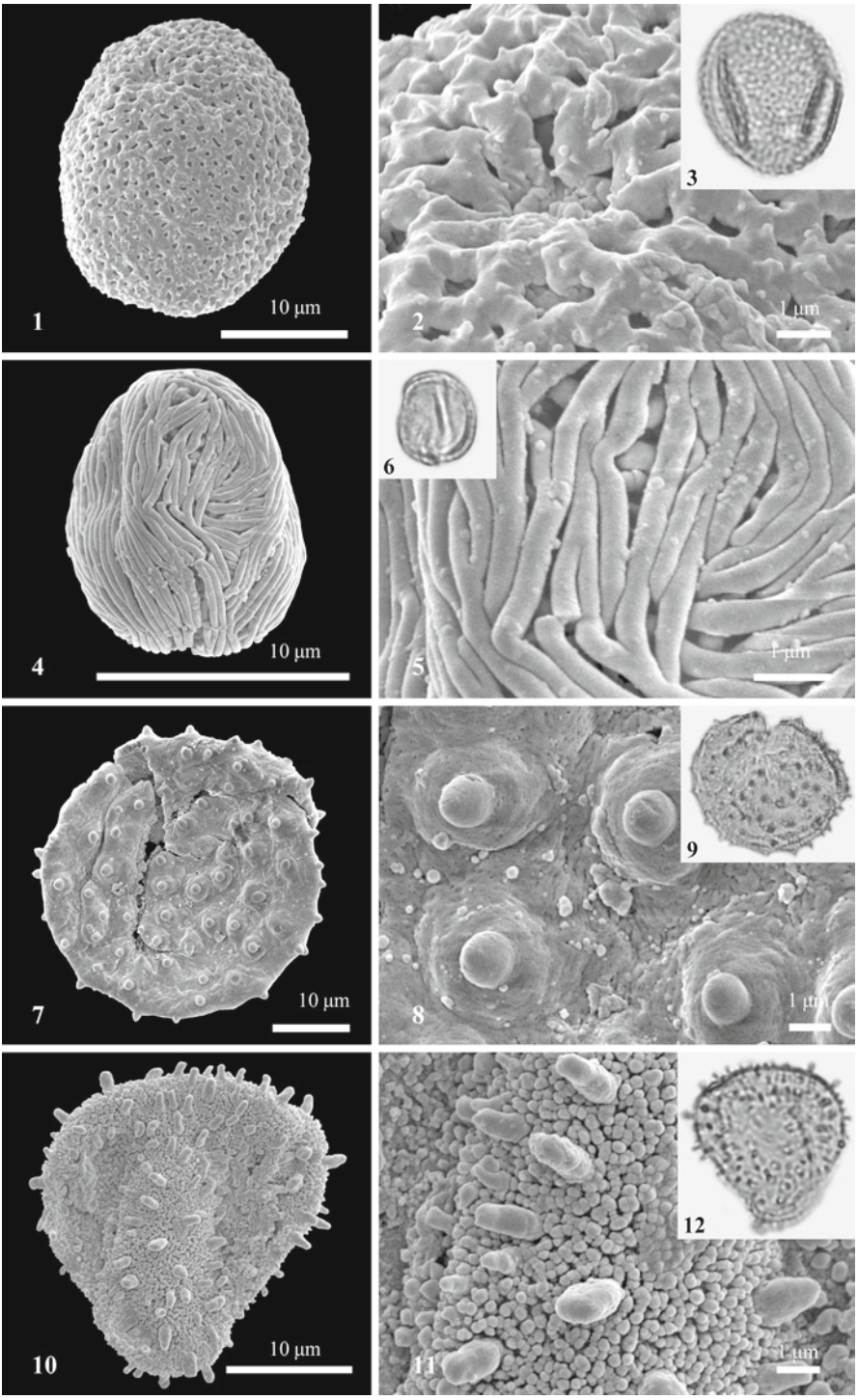



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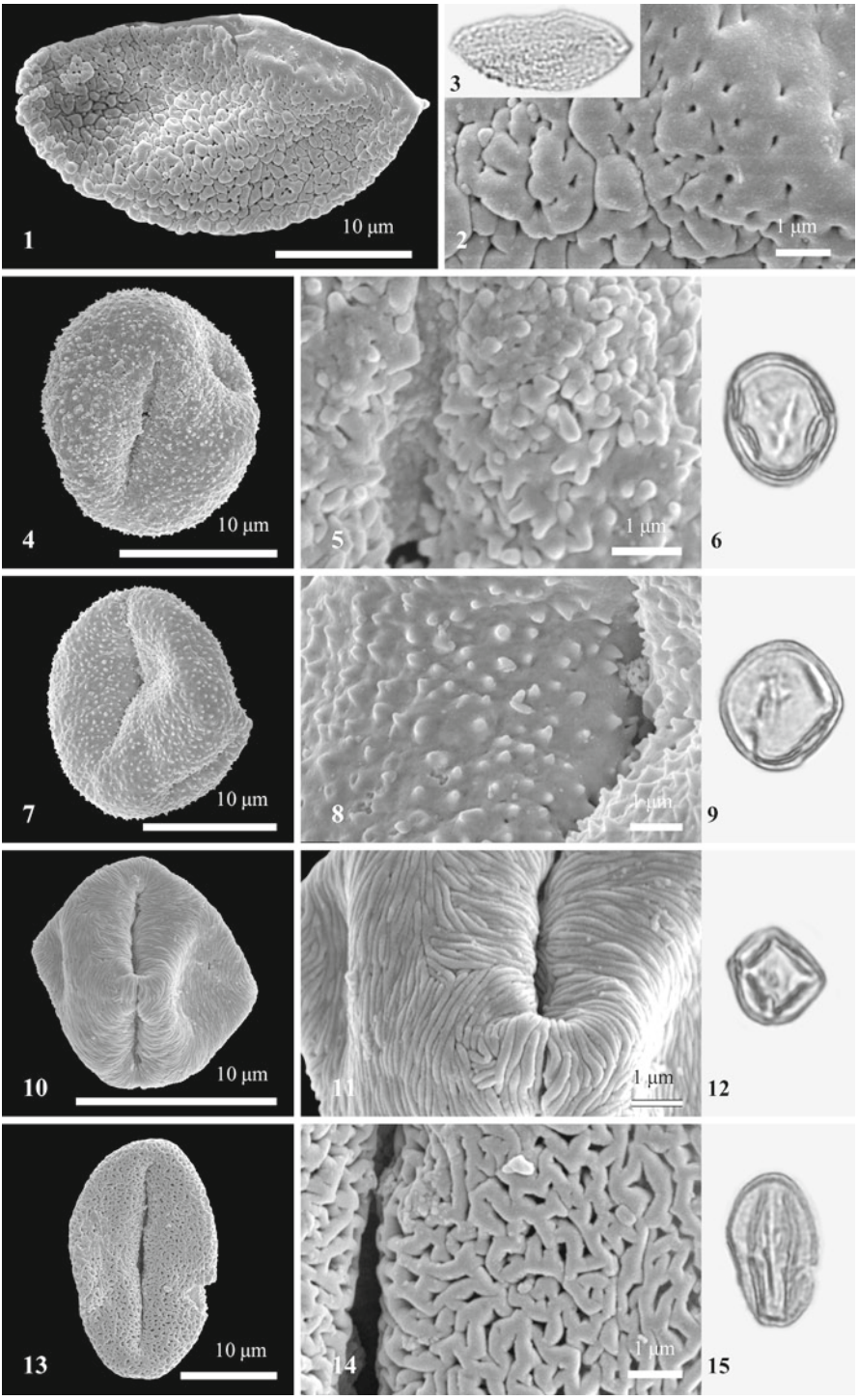

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**Plate 10.30**

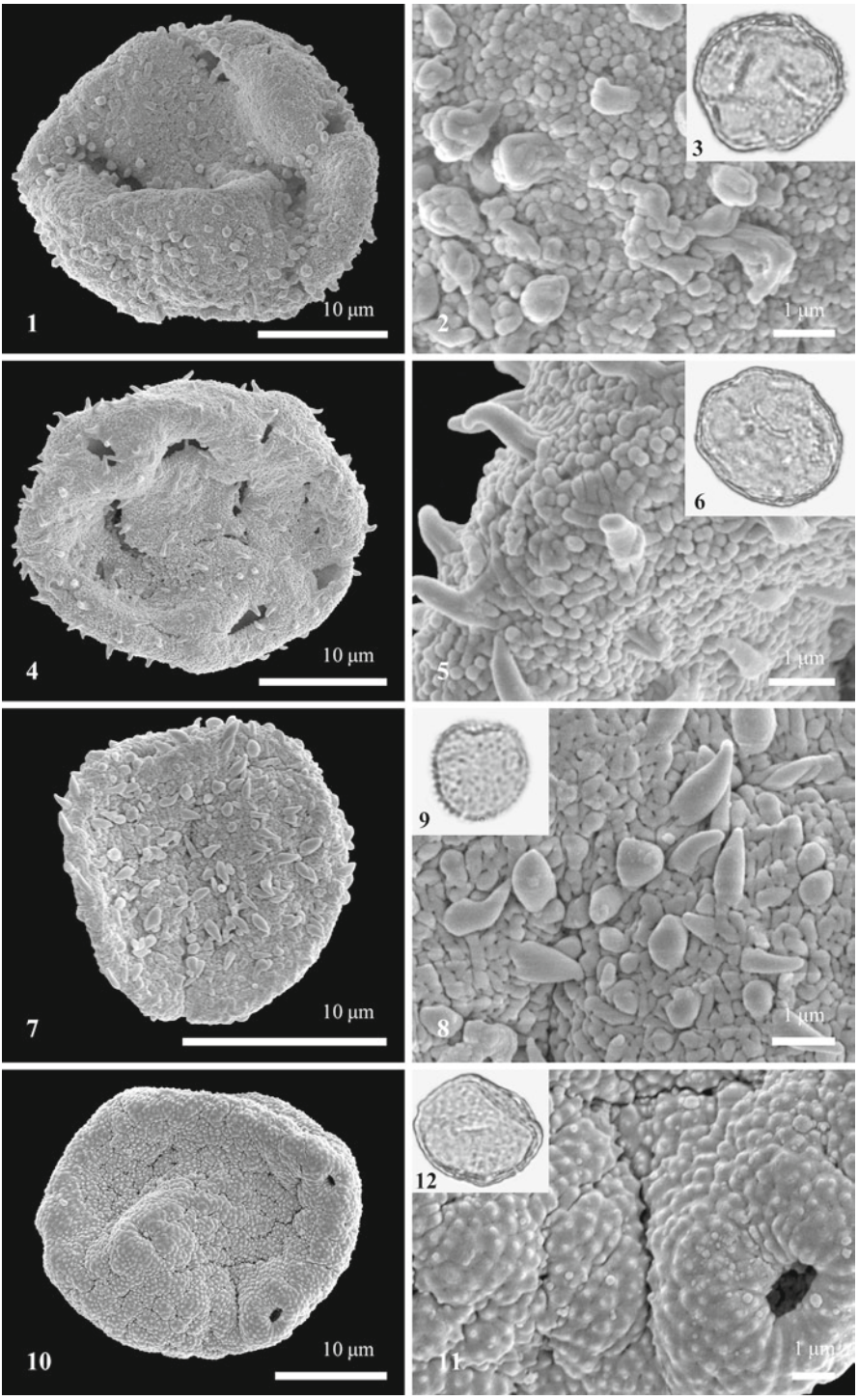



**Plate 10.31**

# Chapter 11
# The Pleistocene Floras (2.4–0.8 Ma) – Shaping the Modern Vegetation of Iceland

**Abstract** The Pleistocene vegetation history of Iceland is closely linked to the onset of large scale northern hemisphere glaciations. The first regional glaciation in Iceland occurred at ca 2.5 Ma (Praetiglian), just before the deposition of the oldest Pleistocene plant-bearing sediments in Iceland (Brekkukambur Formation, 2.4–2.1 Ma). Both the macro- and microfloras of the Brekkukambur Formation are not very well preserved and do not allow detailed interpretations of the palaeoenvironment. However, based on plant and insect remains from the coeval Kap København Formation of northern Greenland, this time marked a last phase of global warmth with boreal forests extending as far north as 82°N. Younger plant-bearing sedimentary formations in Iceland investigated here are ca 1.7, 1.1, and 0.8 Ma in age. They were deposited during interglacials and their floras are very similar to the modern flora of Iceland. It is unclear at the moment whether and how frequently plants survived in Iceland during cold phases. Dispersal mechanisms of plant taxa found in interglacial deposits show that all of them are dispersed by wind or birds over long distances and hence Iceland could have been re-colonized within a rather short period after each cold phase. The composition of the modern flora of Iceland is the result of the dispersal modes and climatic tolerances (competitiveness) of its members. These general conditions appear to have controlled the flora and vegetation of Iceland in a similar way since more than 1.7 million years.

## 11.1 Introduction

Sedimentary rocks containing plant macrofossils from the Pleistocene are rarely found in Iceland. The few known formations have limited extensions and comprise very few localities with well-exposed plant-bearing sediments. The most-studied are the Brekkukambur Formation (ca 2.4–2.1 Ma) on the Hvalfjörður fjord, southwestern Iceland, the Víðidalur Formation (ca 1.7 Ma) in the valley Víðidalur, northern Iceland, the Búlandshöfði Formation (ca 1.1 Ma) on the Snæfellsnes Peninsula, western Iceland, and the Svínafellsfjall Formation (ca 0.8 Ma) in Öræfi, southeastern Iceland (Fig. 11.1).

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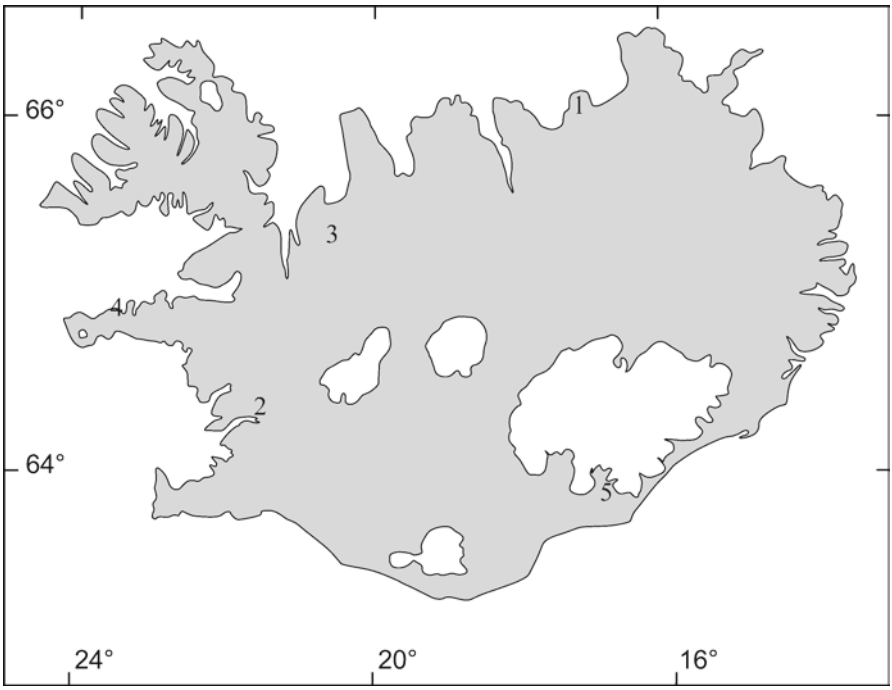



**Fig. 11.1** Map showing studied Pliocene and Pleistocene plant macrofossil localities in Iceland. *1* Tjörnes beds (4.4–2.6 Ma; see Chap. 10), *2* Brekkukambur Formation (2.4–2.1 Ma), *3* Víðidalur Formation (1.7 Ma), *4* Búlandshöfði Formation (1.1 Ma), *5* Svínafellsfjall Formation (0.8 Ma)

The occurrence of plant fossils in the Hvalförður area had been known since the early 1950s. Despite this, to our knowledge, fossils plants of the Brekkukambur Formation have so far only been studied by Akhmetiev et al. (1978). In contrast, the geology of the region and the sedimentary rocks containing the fossils are relatively well-studied by various authors (summarized in Kristinsson 2009).

The Víðidalur Formation and its fossil plants were first discovered in the early 1930s. Soon after, the sediments and their macrofossils were studied in some detail by Líndal (1935, 1939). Even though most of Líndal's work on the sediments in Víðidalur seems to have concentrated on the general geology of the formation (sedimentary type, construction, extension, relative age, etc.), he also described a few macrofossil taxa and provided a short list of pollen (determinations by Knud Jessen). Later studies of the formation have focused mostly on the general geology of the region (Koerfer 1974; Hjartarson 2003), and especially the relative (polarity based) and absolute age of the plant bearing formation (polarity: Hospers 1953; Einarsson 1962; Koerfer 1974; absolute age: Everts et al. 1972; Koerfer 1974; Albertsson 1976; Hjartarson 2003). Additional studies on the macroflora and palynoflora from the Bakkabrúnir locality in Víðidalur were done by Akhmetiev et al. (1978).

Sedimentary rocks on the Snæfellsnes peninsula belonging to the Búlandshöfði Formation were first noted by Thoroddsen (1891). Subsequently, research on this formation has focused mostly on the marine sedimentary rocks which compose most of the formation and their invertebrate fossil fauna (cf. Pjetursson 1904; Bárðarson 1929; Leifsdóttir 1999; Leifsdóttir and Símonarson 2005; Símonarson and Leifsdóttir 2007). The terrestrial units of the formation and the plant fossils, both macrofossils and pollen, were studied to some extent by Áskelsson (1938a, b) and Akhmetiev et al. (1978), who listed each taxon without any description and mostly without photographs.

The Svínafellsfjall Formation was first studied by Nielsen and Noe-Nygaard (1936) and Noe-Nygaard (1953); these studies focused on the tillites (glacial sediments) of the sequence. A few years later, in 1957, farmers hiking across the region found some fragments of plant fossils which they sent to the geologist S. Thorarinsson. He immediately found these plant fragments interesting and between 1957 and 1958 was the first to study the Svínafellsfjall Formation in detail (Thorarinsson 1963). In his work, Thorarinsson gave a thorough description of the whole stratigraphic sequence, including sedimentary and volcanic rock types, construction and origin. In addition, he provided lists of all macrofossil taxa and pollen that had previously been recorded (Thorarinsson 1963). Recently, an even more detailed stratigraphic work was done by Richardson (2006) including detailed descriptions of all sedimentary and volcanic units of the Svínafellsfjall region.

## 11.2 Geological Setting and Taphonomy

### *11.2.1 Brekkukambur Formation, Gljúfurdalur (2.4–2.1 Ma)*

The sedimentary rocks of the Brekkukambur Formation are part of a much thicker volcanic succession of the Gljúfurdalur valley and surrounding areas on the fjord Hvalfjörður including the Miðsandsdalur and Litlasandsdalur valleys along the northern side of the fjord (Fig. 11.2a–c). The sediments accumulated in a caldera lake and are between 2.4 and 2.1 Ma, as estimated from palaeomagnetic correlations of the surrounding lava successions (Kristinsson 2009). The lavas just below the sediments are reversely magnetized and belong to the lowermost part of the Matuyama Chron (Fig. 11.3). Further down the strata, slightly older normally magnetised lavas from the Gauss Chron are present. The boundary between the Pliocene and Pleistocene at 2.58 Ma (Berggren et al. 1995) is present just below the sediments (Kristinsson 2009). The reversely magnetised lavas that erupted during the Réunion Subchron (2.15–2.14 Ma; Berggren et al. 1995) are found just above the sediments. The sediments are therefore believed to have accumulated between 2.4 and 2.1 Ma (Kristinsson 2009). The sedimentary rocks of the Brekkukambur Formation are mostly of fluvial origin (conglomerates and sandstones) and some accumulated in freshwater lake environments (siltstones, claystones); others are of

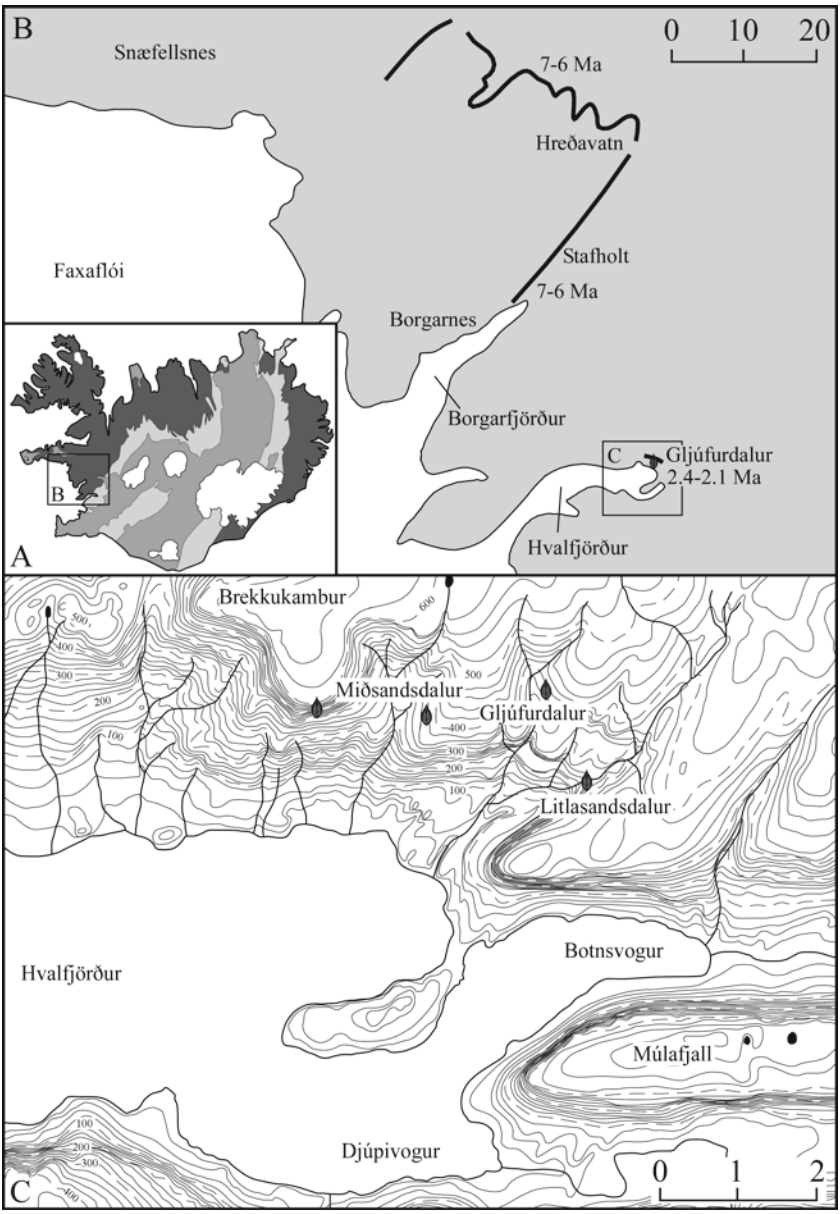



**Fig. 11.2** Map showing fossiliferous localities of the 2.4–2.1 Ma formation. (**a**) bedrock geology (see Fig. 1.10 for explanation), (**b**) extension of sedimentary rock formation, (**c**) Gljúfurdalur area (Geological background modified after Jóhannesson and Sæmundsson 1989; altitudinal lines from Landmælingar Íslands 2000a). Scale bar in kilometres

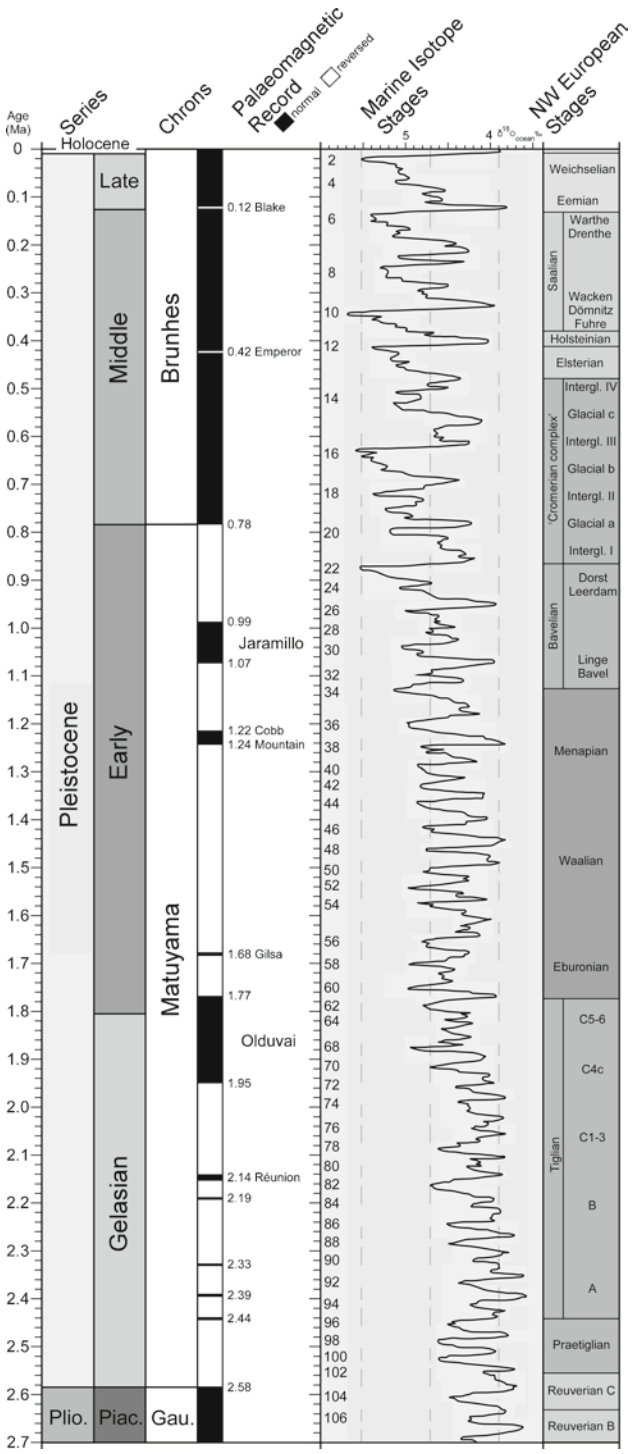



**Fig. 11.3** Chronostratigraphical correlation table for the Late Pliocene to Holocene (Modified after Gibbard and Cohen 2009)

glacial origin (tillites). The clastic fossiliferous sediments are covered by a thick hyaloclastite of subglacial/sublacustrine origin (Harðarson 1978; Kristinsson 2009). Plant macrofossils have been found in sediments at the mountain sides of Miðsandsdalur and, towards the east, in Gljúfurdalur and Litlasandsdalur (Akhmetiev et al. 1978; Harðarson 1978; Fig. 11.2c). The macrofossils, pollen and spores from the sediments were studied by Akhmetiev et al. (1978).

### *11.2.2 Víðidalur Formation, Bakkabrúnir (ca 1.7 Ma)*

The Víðidalur Formation (ca 1.7 Ma) is exposed in the valley Víðidalur, northern Iceland (Fig. 11.4a, b; Plate 11.1). The sediments can be traced for quite some distance along the river Víðidalsá, on both sides of the valley, and towards the mouth of the valley where the river runs into the Húnafjörður fjord (Líndal 1935, 1939; Koerfer 1974). Plant macrofossils are not equally distributed, most of them were found in the outcrop at the Bakkabrúnir cliffs (Fig. 11.4c; Líndal 1935; Akhmetiev et al. 1978). The sediments in Víðidalur are between 10 and 50 m thick (Líndal 1935, 1939; Koerfer 1974; Akhmetiev et al. 1978) and rest on eroded, striated and tilted basalts (unconformity) now believed to have been erupted during the normal polarity interval 3.58–2.58 Ma (Hjartarson 2003), known as the Gauss Chron (Fig. 11.3). The sedimentary rock units at Bakkabrúnir and in the surrounding areas in the Víðidalur valley are composed of glacial deposits (tillites, moraines), various fluvial deposits (conglomerates, sandstones) and lake sediments (sandstones, siltstones and claystones). Part of the erosion of the underlying basalts took place during a glacial advancement; the glacial sediments are believed to have accumulated during the same glacial period that caused the erosion and left the striation on the lava surface. The fluvial and lake deposits then formed in the following interglacial period when the glaciers retreated.

The Víðidalur Formation was deposited during the same time as many other sedimentary units in the surroundings of the Víðidalur valley, the Vatnsdalur valley, the Skagi Peninsula and the inland of the Skagafjörður fjord (Koerfer 1974; Hjartarson 2003). The sediments belonging to these constructions are commonly covered by reversely polarized basalts that are now known to be 1.66–1.25 Ma (Ar/Ar dates by Hjartarson 2003) and represent part of the Matuyama Epoch (Fig. 11.3). The sediments below the basalts are therefore considered to be ca 1.7 Ma.

### *11.2.3 Búlandshöfði Formation, Stöð (ca 1.1 Ma)*

The Búlandshöfði Formation (ca 1.1 Ma; Albertsson 1976; Einarsson 1977) is exposed on the northern side of the Snæfellsnes Peninsula, Western Iceland (Fig. 11.5a, b; Plate 11.15). The sedimentary rocks of this formation can be traced from Mount Kirkjufell to the east and over to Búlandshöfði to the west.

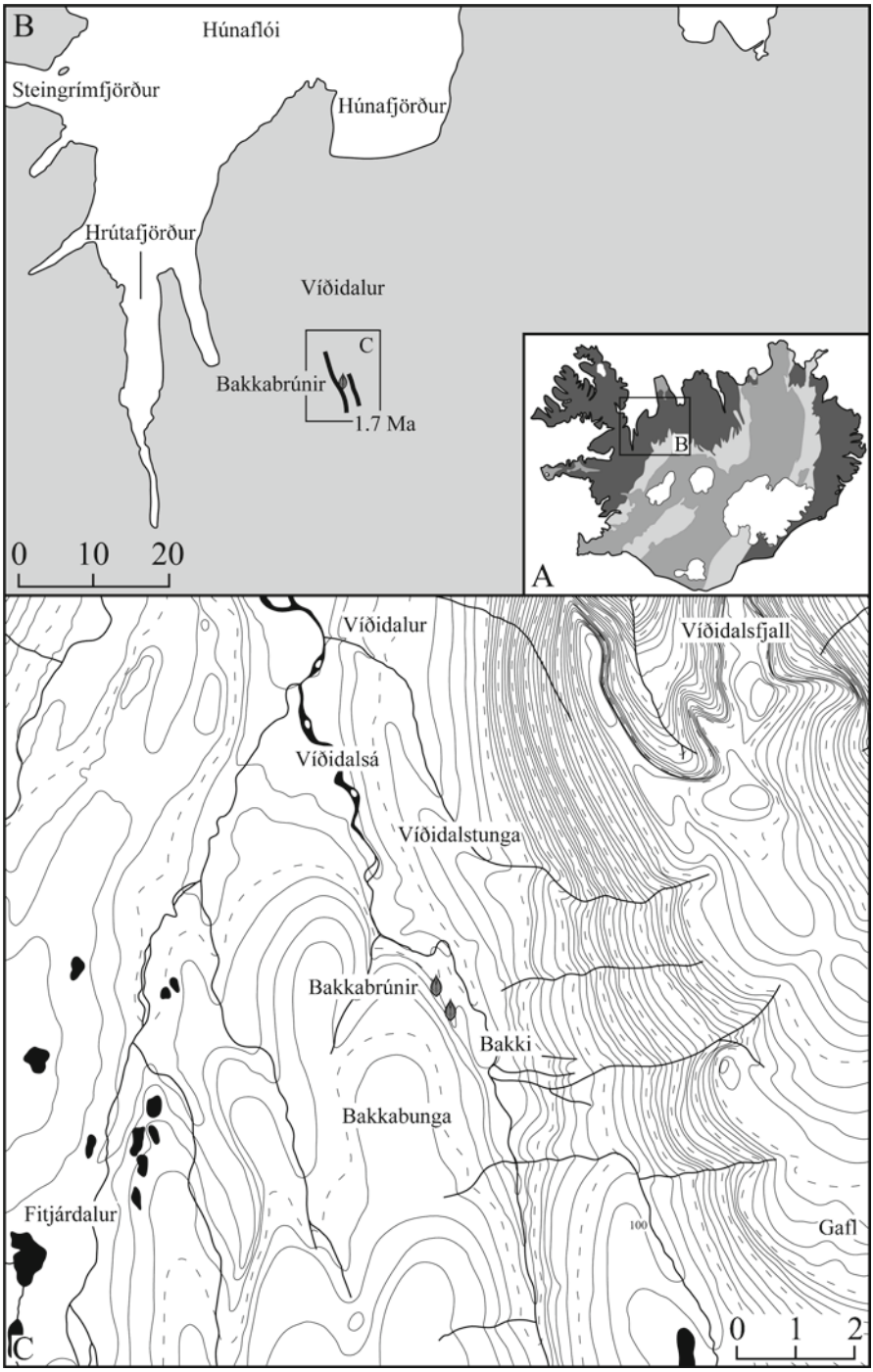



**Fig. 11.4** Map showing fossiliferous locality of the 1.7 Ma formation. (**a**) bedrock geology (see Fig. 1.10 for explanation), (**b**) extension of sedimentary rock formation, (**c**) Bakkabrúnir area (Geological background modified after Jóhannesson and Sæmundsson 1989; altitudinal lines from Landmælingar Íslands 1997, 2000b). Scale bar in kilometres

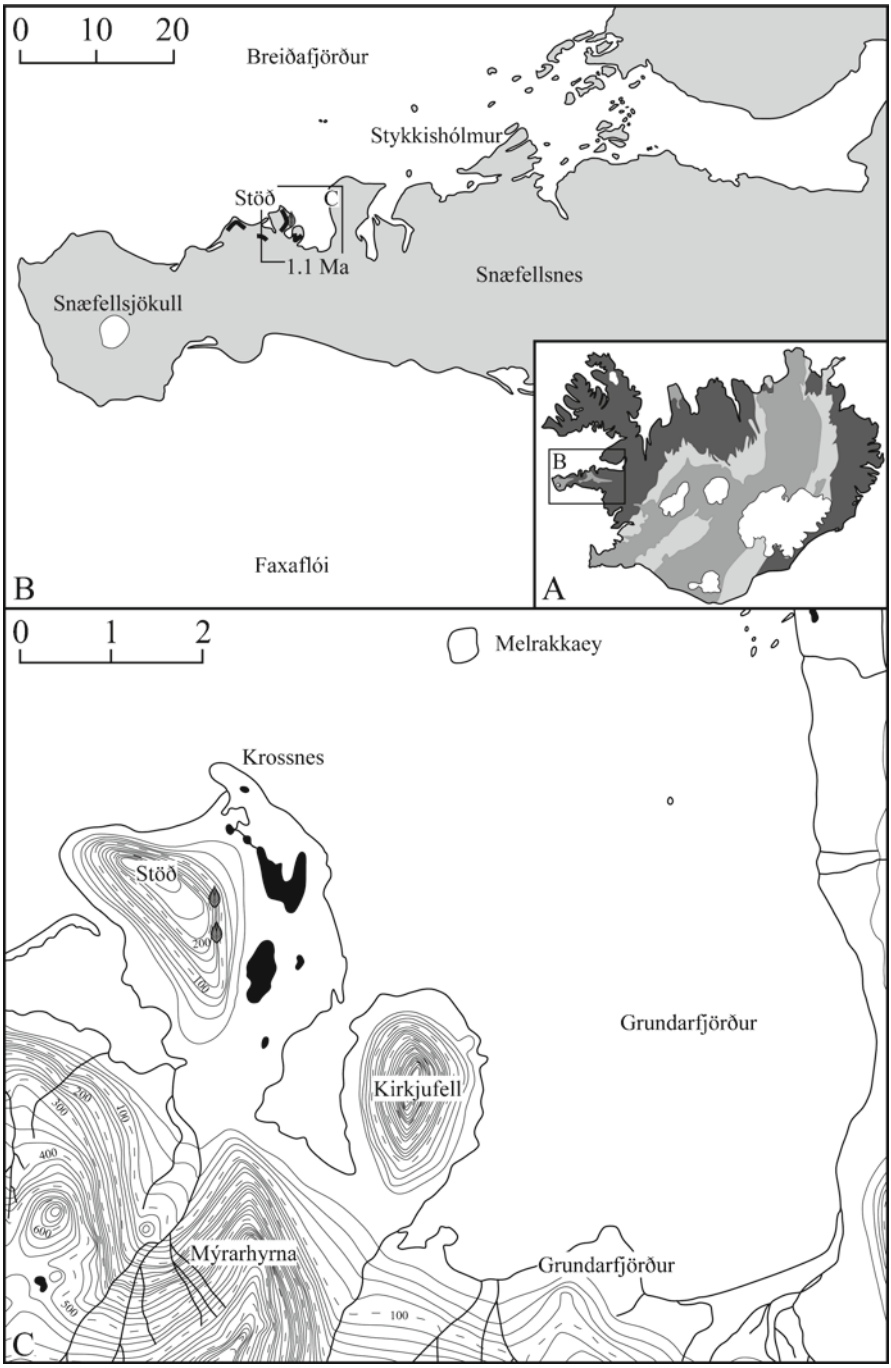



**Fig. 11.5** Map showing fossiliferous locality of the 1.1 Ma formation. (**a**) bedrock geology (see Fig. 1.10 for explanation), (**b**) extension of sedimentary rock formation, (**c**) Stöð area (Geological background modified after Jóhannesson and Sæmundsson 1989; altitudinal lines from Landmælingar Íslands 1990a, 2004). Scale bar in kilometres

The formation is up to 50 m thick and rests on eroded and glacially striated Tertiary basaltic lavas of reverse or normal polarity (Pjetursson 1904; Hospers 1953). The sedimentary rocks are covered by reversely polarized basaltic lavas from the Matuyama Chron (Leifsdóttir 1999) that are approximately 1.1 Ma (Albertsson 1976; Einarsson 1977). The lavas are of the same age as the uppermost unit of the sedimentary rock sequence, and the sedimentary rocks as well as the lavas were formed during a glacial and the following interglacial stage (Leifsdóttir 1999).

The lower part of the sedimentary rock sequence (Kirkjufell locality, Stöð locality, Skerðingsstaðafjall locality, Búlandshöfði locality) is composed of pebbly diamicton with dropstones, flat-bedded conglomerates and sandstones. It is a glacier-marine deposit with arctic marine invertebrate fossils occurring mostly in the diamictite (Leifsdóttir 1999; Leifsdóttir and Símonarson 2005; Símonarson and Leifsdóttir 2007). The upper part of the sequence is for most parts composed of shallow water, flat-bedded marine sandstones and conglomerates with thermophilic invertebrate fossils (Búlandshöfði locality), except for on Mount Stöð (Stöð locality) where coarse-grained deltaic sandstones, conglomerates, and fine grained lacustrine sandstones and siltstones accumulated in a lake or lagoon close to the coastline (Leifsdóttir 1999; Leifsdóttir and Símonarson 2005; Símonarson and Leifsdóttir 2007). The Stöð locality (Fig. 11.5c) is the only outcrop of this formation where plant macrofossils can be found.

### *11.2.4 Svínafellsfjall Formation, Svínafell (ca 0.8 Ma)*

The Svínafellsfjall Formation (0.8 Ma; Helgason 2007) has a relative short lateral extension of ca 4 km (Fig. 11.6c; Plate 11.30). The only accessible exposure is located in the Öræfi region, southeastern Iceland, close to the Vatnajökull glacier (Fig. 11.6a, b). The sediments and associated volcanic rocks form part of Mount Svínafellsfjall, hence the formations name. Mount Svínafellsfjall is bordering the Öræfajökull (part of Vatnajökull) and it is flanked by two outlet glaciers, the Svínafellsjökull and Virkisjökull, on the mountains' northwestern and southeastern sides.

The fossiliferous sediments at Svínafell rest on glacially eroded basalt surface. The ages of these basalt lavas vary, but all of them are considered to be of Pleistocene age (Helgason 2007). The lowermost of these lavas are reversely magnetized and are believed to have formed during the Matuyama Chron (Fig. 11.3), while the uppermost lavas are normally magnetised and most likely formed during the Jaramillo Subchron 1.07–0.99 Ma (Albertsson 1976; Fig. 11.3).

The overlaying fine-grained (silt- and sandstones) sediments containing plant fossils are over 120 m thick, and accumulated in a lake environment at close distance to a glacier as evidenced by the numerous dropstones within the sediments (Thorarinsson 1963; Richardson 2006). In the uppermost part, the plant bearing sediments were eroded by tillites. Following the tillites is a thin sequence of basaltic lava flows. Then again, a hiatus (erosion) occurs in the stratigraphic succession and the lavas are overlain by pillow lavas, breccias and various hyaloclastites (tuffs) of

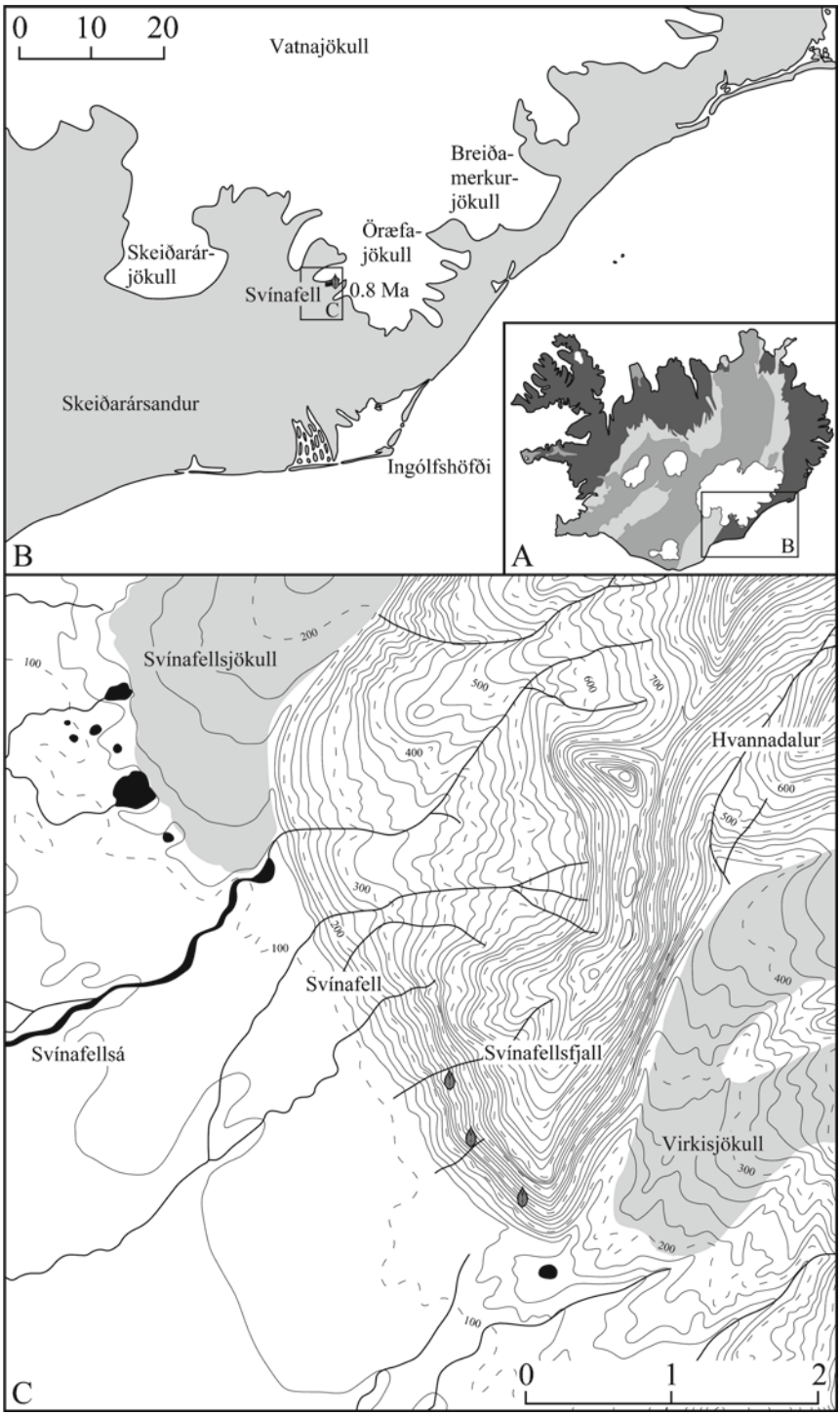



**Fig. 11.6** Map showing fossiliferous locality of the 0.8 Ma formation. (**a**) bedrock geology (see Fig. 1.10 for explanation), (**b**) extension of sedimentary rock formation, (**c**) Svínafell area (Geological background modified after Jóhannesson and Sæmundsson 1989; altitudinal lines from Landmælingar Íslands 1990b). Scale bar in kilometres

subglacial volcanic origin. Then, still another hiatus (erosional surface) is documented in the stratigraphic column, followed by a second tillite and a basaltic lava sequence (Thorarinsson 1963; Richardson 2006).

The sediments and volcanic construction contain some information about the environmental and climatic changes in the region during the formation. The basalts below the plant bearing sediments clearly formed during a warm, more or less ice-free, period. The climate then became cooler and glacial advance took place eroding into the lavas and forming the deep depression containing the lake sediments. As the glacier retreated, following climate warming, the basin was filled with melt water and a lake formed. The lake gradually became shallower as the basin was filled with fine-grained clastic sediments. Based on the mean varve thickness and the total thickness of the lake sediments, Richardson (2006) estimated the time for deposition of the lake sediments between 13,000 and 30,000 years for the whole 120 m thick lacustrine sequence. After some time the climate again became cooler and glaciers re-advanced eroding the top of the lake sediments and forming the first tillites. When the glaciers had retreated again, the following lava flow series formed during an interglacial period. Two other glacial-interglacial cycles have been documented in the following stratigraphic sections (cf. Thorarinsson 1963; Richardson 2006).

The age of the plant-bearing sediments at Svínafell has been debated for some years; Thorarinsson (1963) suggested a Mindel-Riss interglacial age (corresponding to the Holsteininan interglacial, ca 0.4 Ma), whereas Einarsson (1968, 1971) suggested that the sediments formed during the third last interglacial period in the early Brunhes Chron (Fig.11.3). Albertsson (1976) concluded that the sediments were deposited sometime between post-Jaramillo and the early Brunhes glaciation (Elsterian; Fig. 11.3); this he based on absolute K/Ar dating of 0.6–0.4 Ma for the lavas overlaying the fossiliferous sediments. Recently, more reliable absolute dating by Helgason (2007) gave 0.76–0.59 Ma for the same lava series positioned above the sediments. This would suggest that the fossiliferous lake sediments close to the bottom of the Svínafellsfjall sequence are ca 0.8 Ma.

## 11.3 Floras, Faunas, and Palaeoenvironments

With the exception of very few taxa (*Pinus*, *Alnus viridis*, *Myrica gale*) the set of taxa encountered in Pleistocene sedimentary rock formations equals the modern flora of Iceland. While *Pinus* and *Alnus viridis* occur in all Pleistocene formations investigated here, *Myrica* has not been reported from floras younger than 1.7 Ma. Iceland today comprises three distinct vegetation zones. The most favourable parts of Iceland in the southwest and south and some interior fjords and valleys in the east and north belong to the middle and northern boreal zones. Oceanic lowlands are dominated by coastal birch woodland with *Sorbus aucuparia* and *Empetrum* and partly *Calluna* heaths. A few southerly plants such as *Fragaria vesca* Coville and *Prunella vulgaris* L. occur here. From about 300 to 400 m a. s. l., treeless areas reach up to the highest ice-free summits. The low-alpine belt consists of meadows

and dwarf-shrub heaths; at higher elevations, the vegetation becomes patchier and vascular plants decrease; lichens, mosses and hepatics are dominating and large areas are bare rock, fields of large boulders or snow accumulations (Sjörs 2004). The situation encountered in the Pleistocene floras of Iceland is markedly similar to the one described above.

### *11.3.1 Brekkukambur Formation, Gljúfurdalur (2.4–2.1 Ma)*

We spent only a brief time at Hvalfjörður and collected a small amount of macrofossils. Hence, the following description is based on Akhmetiev et al. (1978). The Lower Pleistocene deposits of this area are poor in organic remains (Table 11.1). The macroflora is dominated by leaf remains of *Salix glauca* L. *fossilis* and *Dryas octopetala*. The palynological record is dominated by *Alnus*, *Salix*, *Betula* spp. and spores of bryophytes. Herbaceous taxa are rare in the pollen sample analysed by Akhmetiev et al. (1978).

**Table 11.1** Taxa recorded for the 2.4–2.1 Ma Gljúfurdalur flora

| Brekkukambur Formation 2.4–2.2 Ma<br>Taxa (From Akhmetiev et al. 1978) | Pollen | Leaves | DM |
|---|---|---|---|
| Bryophyta | | | |
| Bryophyta | + | | 1a |
| Betulaceae | | | |
| *Alnaster virdis* (Spach.) Czerep. *fossilis* | + | + | 1a |
| *Betula* sp. | + | + | 1a |
| *Betula nana* L. | + | | 1a |
| Caryophyllaceae | | | |
| Caryophyllaceae | + | | 1b |
| Chenopodiaceae | | | |
| Chenopodiaceae gen. et spec. indet. | + | | 1b |
| Ericaceae | | | |
| *Vaccinium uliginosum* L. | | + | 1b |
| Gramineae | | | |
| Gramineae | + | | |
| Rosaceae | | | |
| *Dryas octopetala* L. | | + | 1a |
| Salicaceae | | | |
| *Salix glauca* L. *foss.* | (+) | + | 1a |
| *Salix lanata* L. *foss.* | (+) | + | 1a |
| *Salix phylicifolia* L. *foss.* | (+) | + | 1a |

*RP* reproductive structure, *DM* dispersal mode, *L* leafy axis, *A* fruit attached to leafy axis, *D* fruit dispersed, + organ included in a particular taxon, + original description of species based on this organ, (+) organ belonging to genus but uncertain to which of the species, (+)*2* indicating number of pollen types possibly belonging to the eponymous morphotaxon, *1a* wind long distance (anemochory), *1b* bird long distance (endozoochory), *2a* wind short distance (anemochory), *2b* animals short distance (exozoochory), 3 dyschory

### 11.3.2 Víðidalur Formation, Bakkabrúnir (1.7 Ma)

The macrofossil assemblage from Bakkabrúnir is dominated by *Alnus* aff. *A. viridis* and *Polygonum viviparum* (Table 11.2). *Salix, Betula*, *Dryas* and *Vaccinium* are less abundant among the macrofossils. In contrast, the palynological record is fairly rich in taxa. Combined with the macrofossil record, the Bakkabrúnir flora is dominated by herbaceous plants (19 taxa). Woody angiosperms and ferns and fern allies are represented by seven taxa each and conifers by a single taxon (*Pinus*; Fig. 11.7; Plates 11.2–11.14). Most of the taxa in the Bakkabrúnir flora are also present in the modern flora of Iceland. Exceptions are *Pinus*, *Alnus viridis* (Chaix) DC., *Myrica* and *Trollius*.

**Table 11.2** Taxa recorded for the 1.7 Ma Bakkabrúnir flora

| Víðidalur Formation 1.7 Ma<br>Taxa | Pollen | Leaves | RP | Other | DM |
|---|---|---|---|---|---|
| Bryophyta | | | | | |
| *Sphagnum* sp. | + | | | | 1a |
| Lycopodiaceae | | | | | |
| *Lycopodium* | + | | | | 1a |
| *Huperzia* sp. | + | | | | 1a |
| Osmundaceae | | | | | |
| *Osmunda* sp. | + | | | | 1a |
| Polypodiaceae | | | | | |
| Polypodiaceae gen. et spec. indet. 1 | + | | | | 1a |
| Incertae sedis – unassigned spores | | | | | |
| Trilete spore, fam., gen. et spec. indet. 6 | + | | | | 1a |
| Trilete spore, fam., gen. et spec. indet. 7 | + | | | | 1a |
| Pinaceae | | | | | |
| *Pinus* sp. 1 (Diploxylon type) | + | | | | 2a |
| Asteraceae | | | | | |
| *Artemisia* sp. 1 | + | | | | 1a |
| Asteraceae gen. et spec. indet. 1 | + | | | | 1a |
| Betulaceae | | | | | |
| *Alnus* aff. *viridis* | (+)2 | + | | | 1a |
| *Betula nana* x *pubescens* | + | + | | | 1a |
| Caryophyllaceae | | | | | |
| Caryophyllaceae gen. et spec. indet. 5 | + | | | | 1b |
| Caryophyllaceae gen. et spec. indet. 6 | + | | | | 1b |
| Caryophyllaceae gen. et spec. indet. 7 | + | | | | 1b |
| Cyperaceae | | | | | |
| *Kobresia* sp. | + | | | | 1b |
| Ericaceae | | | | | |
| Ericaceae gen. et spec. indet. 8 | + | | | | 1b |
| *Vaccinium* cf. *uliginosum* | | + | | | 1b |
| Menyanthaceae | | | | | |
| *Menyanthes* sp. | + | | | | 1b |

(continued)

**Table 11.2** (continued)

| Víðidalur Formation 1.7 Ma<br>Taxa | Pollen | Leaves | RP | Other | DM |
|---|---|---|---|---|---|
| Myricaceae | | | | | |
| *Myrica* sp. | + | | | | 1b |
| Polygonaceae | | | | | |
| *Polygonum* sect. *Aconogonon* sp. | + | | | | 1b |
| *Polygonum viviparum* | + | + | | | 1b |
| *Rumex* sp. | + | | | | 1b |
| Ranunculaceae | | | | | |
| *Ranunculus* sp. 3 | + | | | | 1b |
| *Thalictrum* sp. 2 | + | | | | 1b |
| *Thollius* sp. | + | | | | 1b |
| Ranunculaceae gen. et spec. indet. 2 | + | | | | 1b |
| Ranunculaceae gen. et spec. indet. 6 | + | | | | 1b |
| Rosaceae | | | | | |
| *Dryas octopetala* | | + | | | 1a |
| *Fragaria* sp. | + | | | | 1b |
| *Sanguisorba* sp. | + | | | | 1b, 2a |
| Rosaceae gen. et spec. indet. 13 | + | | | | 1b |
| Salicaceae | | | | | |
| *Salix* sp. B (*S. arctica* type) | (+)2 | + | | | 1a |
| Saxifragaceae | | | | | |
| *Saxifraga* sp. | + | | | | 1a |
| Incertae sedis – Magnoliophyta | | | | | |
| Pollen type 28 | + | | | | ? |

*RP* reproductive structure, *DM* dispersal mode, *L* leafy axis, *A* fruit attached to leafy axis, *D* fruit dispersed, + organ included in a particular taxon, (+) organ belonging to genus but uncertain to which of the species, (+)*2* indicating number of pollen types possibly belonging to the eponymous morphotaxon, *1a* wind long distance (anemochory), *1b* bird long distance (endozoochory), *2a* wind short distance (anemochory), *2b* animals short distance (exozoochory), *3* dyschory

*Alnus viridis* occurs in various subspecies across the northern hemisphere; the populations of subsp. *crispa* (Aiton) Turrill are located most closely to Iceland in southwestern Greenland. Subsp. *viridis* is found in European mountains and subsp. *fruticosa* (Rupr.) Nyman from northern Russia to northern Asia (Meusel et al. 1965). The migration to Iceland could have happened both from northwestern Russia and from Greenland. *Alnus viridis* is recorded from all the Pleistocene formations studied here; hence its absence from the modern flora of Iceland may be the result of competition during postglacial expansion rather than climatic intolerance. *Trollius europaeus* (globeflower) has a wide distribution range from the mountain ranges of the Iberian Peninsula and Italy to northern Scandinavia and the northern Ural Mountains (Polar Ural). It is also found on the British Isles but absent from the Faeroe Islands. *Trollius* has its last occurrence in Iceland in the 1.7 Ma

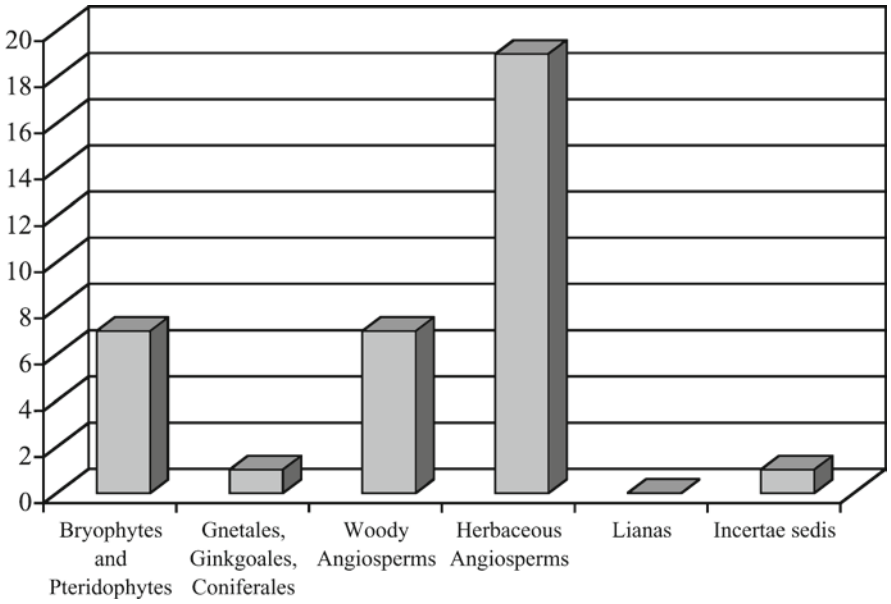



**Fig. 11.7** Distribution of life forms and higher taxa among the plants from the 1.7 Ma formation. Height of columns indicates number of taxa

sedimentary formation, which could be explained by the highly complex pollination ecology of this plant. Globeflowers are exclusively pollinated by flies whose larvae feed only on their seeds (e.g. Despres et al. 2007). *Myrica gale* has a western European distribution from Spain to northern Norway. It arrived in Iceland before 9–8 Ma and had its last occurrence in the 1.7 Ma formation. As in the case of *Alnus*, competition not allowing isolated populations to expand from glacial refugia may have been the reason for the absence of *Myrica* in Iceland after 1.7 Ma rather than climatic intolerance.

*Fragaria* occurs in the 4.3–1.7 Ma sedimentary rock formations in Iceland and is a rare element of the modern Icelandic flora. According to Sjörs (2004) a number of species, such as *Fragaria vesca*, *Galium boreale* L. and *Prunella vulgaris*, are distinctive southerly elements in the modern vegetation of Iceland that are not typical of the middle and northern boreal zones. This may suggest that the climate during deposition of the 1.7 Ma formation was very similar to the modern climate favouring a forest tundra in relatively mild lowlands. Based on the plant fossils recovered, the vegetation consisted of aquatic and swamp vegetation that were closely connected to wet shrublands (Table 11.3). Well-drained areas were occupied by meadows with small shrubs of *Myrica*, *Salix* and Ericaceae. Microclimatically favoured areas provided habitats for forest tundra with an herbaceous understorey. Here, southerly plants such as *Fragaria* might have dwelled along the forest edges (Figs. 11.8 and 11.9). Edaphically dry rocky outcrops may have been occupied by *Pinus*.

**Table 11.3** Vegetation types ca 1.7 Ma ago

Vegetation types at the Bakkabrúnir locality

**Aquatic vegetation**
*Menyanthes* sp.

**Swamp vegetation**
*Osmunda* sp.
*Kobresia* sp.
*Menyanthes* sp.
*Myrica* sp.

**Wet shrublands**
*Sphagnum* sp.
*Osmunda* sp.
*Alnus* aff. *viridis*
Asteraceae gen. et spec. indet. 1
*Betula nana* x *pubescens*
Ericaceae gen. et spec. indet. 8
*Myrica* sp.
*Polygonum viviparum*
*Salix* sp. 4, 5
*Trollius* sp.
*Vaccinium* cf. *uliginosum*

**Meadows**
*Sphagnum* sp.
*Huperzia* sp.
*Lycopodium* sp.
*Artemisia* sp. 1
Asteraceae gen. et spec. indet. 1
Caryophyllaceae gen. et spec. indet. 5–7
Ericaceae gen. et spec. indet. 8
*Myrica* sp.
*Polygonum* sect. *Aconogonon* sp.
*Polygonum viviparum*
Ranunculaceae gen. et spec. indet. 2, 6
*Ranunculus* sp. 3
Rosaceae gen. et spec. indet. 13
*Rumex* sp.
*Salix* sp. B (*S. arctica* type)
*Sanguisorba* sp.
*Thalictrum* sp. 2
*Trollius* sp.
*Vaccinium* cf. *uliginosum*

**Forest tundra**
*Sphagnum* sp.
*Lycopodium* sp.
*Pinus* sp. 1
*Alnus* aff. *viridis*
*Betula nana* x *pubescens*
*Vaccinium* cf. *uliginosum*
*Polygonum viviparum*
*Dryas octopetala*
*Fragaria* sp. 1
*Salix* sp. B (*S. arctica* type)

**Rocky outcrop forest**
*Huperzia* sp.
*Pinus* sp. 1
*Dryas octopetala*
*Fragaria* sp. 1
*Sanguisorba* sp.
*Saxifraga* sp.

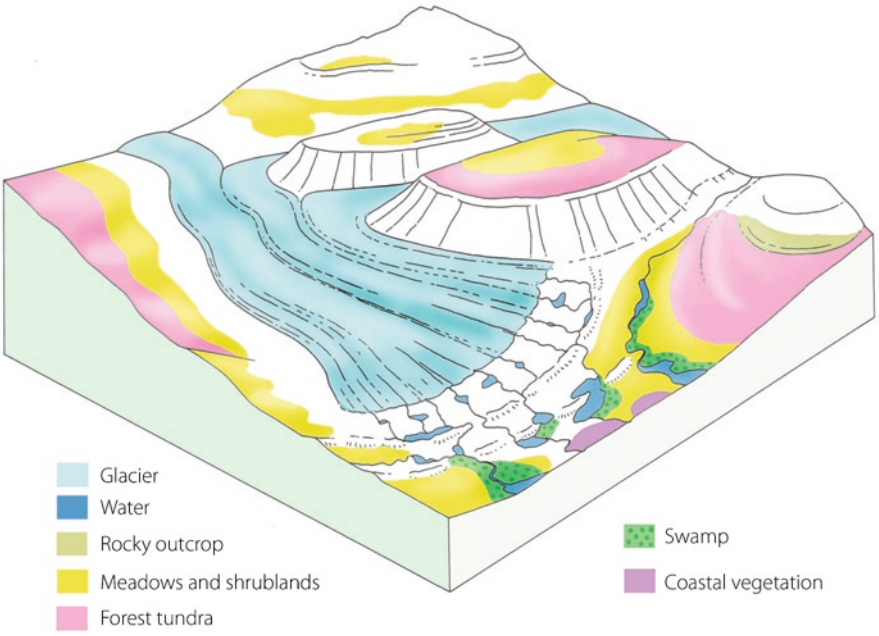



**Fig. 11.8** Schematic block diagram showing palaeo-landscape and vegetation types for Pleistocene interglacials of Iceland

### *11.3.3 Búlandshöfði Formation, Stöð (1.1 Ma)*

During the end of a cold phase (marine isotope stage 32), about 1.1 Ma (Albertsson 1976; Einarsson 1977), glaciers on the Snæfellsnes Peninsula retreated and the sea level rose. The glaciomarine sediments composing the lower part of the Búlandshöfði Formation (seen at the Kirkjufell, Stöð, Skerðingsstaðafjall and Búlandshöfði localities) accumulated during a transgression. Subsequently, continuous glacial retreat and uplift of land led to the accumulation of the terrestrial and lake/lagoon sequence known from the Stöð locality and to the more intertidal environments with a thermophilic littoral marine fauna. This fauna lived at the beginning of an interglacial period when the sea temperature had increased considerably (Leifsdóttir 1999; Símonarson and Leifsdóttir 2007).

The marine faunal assemblages in the Búlandshöfði Formation contain 43 species of marine molluscs and barnacles (Símonarson and Leifsdóttir 2007). Molluscs in the lower Búland Member belong to the *Macoma-Portlandia* bottom infaunal assemblages, in which the bivalve *Portlandia arctica* (Gray) plays a prominent role. It is a cold water species not living in Iceland today and strongly indicative of arctic sea temperatures during deposition (Leifsdóttir 1999). The number of species decreases upward in the Búland Member, especially the more arctic ones, indicating increasing sea temperatures. In the upper Höfði Member of the Búlandshöfði Formation, the faunal assemblages are more thermophilic and contain littoral

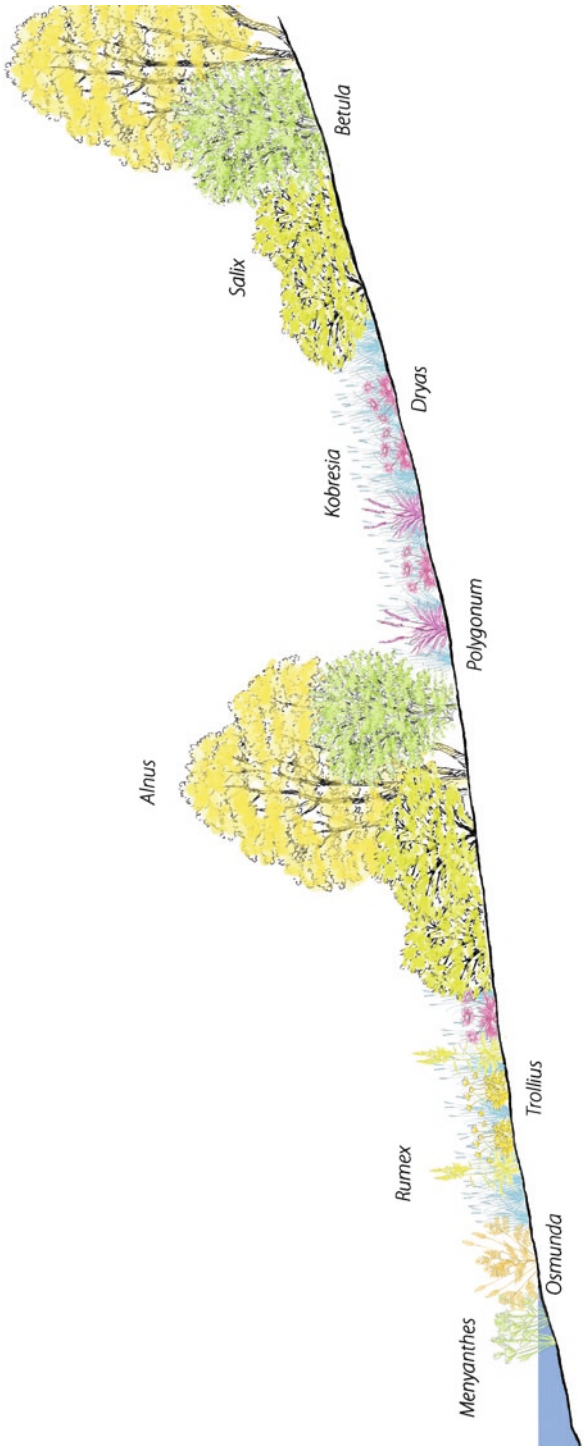



**Fig. 11.9** Schematic transect of aquatic vegetation, meadows and forest tundra, 1.7 Ma in Iceland

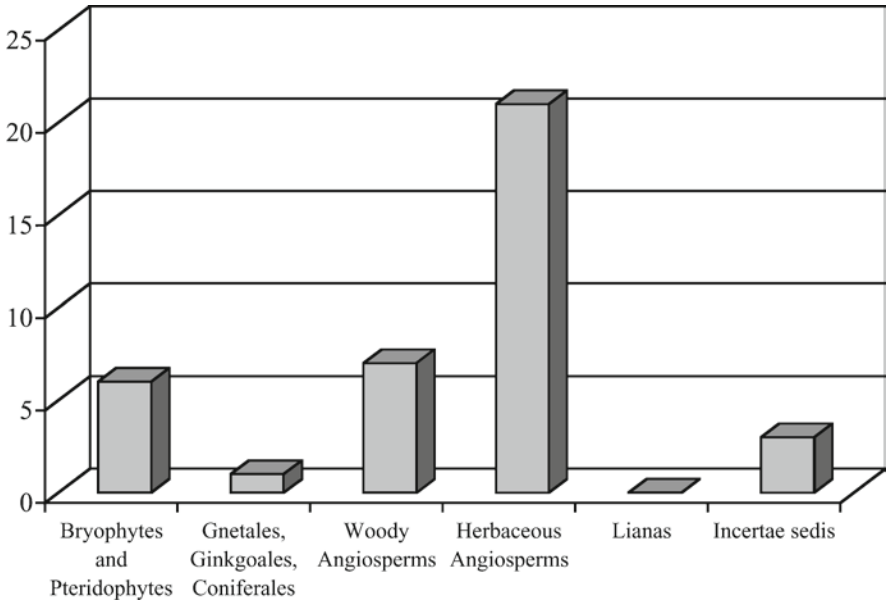



**Fig. 11.10** Distribution of life forms and higher taxa among the plants from the 1.1 Ma formation. Height of columns indicates number of taxa

species such as *Littorina littorea* (L.), *Nucella lapillus* (L.), *Mytilus edulis* L. and *Semibalanus balanoides* (L.) (Leifsdóttir 1999). Molluscs belong to the *Mytilus-Littorina* epifaunal assemblages indicating boreal sea temperatures similar to the present ones in the area (Símonarson and Leifsdóttir 2007).

Stefánsson (1991) demonstrated a correlation between the sea surface temperatures and air temperatures around Iceland. The plant-bearing sediments of the Stöð Member are contemporaneous with the Höfði Member (Símonarson and Leifsdóttir 2007) and allow direct comparison between marine and terrestrial palaeoecological signals. The flora of Stöð comprises 38 taxa, most of which are herbaceous angiosperms (21 taxa). The remaining taxa comprise woody angiosperms (seven taxa), ferns and fern allies (six taxa) and a single conifer (*Pinus*; Fig. 11.10 and Table 11.4; Plates 11.16–11.29). The composition is similar to the one found in Bakkabrúnir except for the absence of *Myrica*, *Fragaria* and *Trollius*. Instead, pollen of *Mercurialis perennis* L. was reported in the Stöð assemblage. *Mercurialis* is missing in the modern flora of Iceland. It has a large range in Central and Eastern Europe extending into temperate areas in Southern Europe, Northern Africa and northern Iran to the east. In western Norway isolated populations are found close to the Polar Circle (Anderberg and Anderberg 2010). This distribution pattern may point to hindered postglacial expansion due to competition. Another species that is absent from the modern Icelandic flora is *Plantago coronopus* L. While having a large distribution from the Sahara to southern Scandinavia, the British Isles and the Faeroes (Anderberg and Anderberg 2010), the distribution of this halophyte may to some degree be controlled by edaphic factors.

**Table 11.4** Taxa recorded for the 1.1 Ma Stöð flora

| Búlandshöfði Formation 1.1 Ma<br>Taxa | Pollen | Leaves | RP | DM |
|---|---|---|---|---|
| Lycopodiaceae | | | | |
| *Lycopodium* | + | | | 1a |
| *Huperzia* sp. | + | | | 1a |
| Lycopodiaceae gen. et spec. indet. 2 | + | | | 1a |
| Osmundaceae | | | | |
| *Osmunda* sp. | + | | | 1a |
| Polypodiaceae | | | | |
| Polypodiaceae gen. et spec. indet. 1 | + | | | 1a |
| Incertae sedis – unassigned spores | | | | |
| Trilete spore, fam., gen. et spec. indet. 8 | + | | | 1a |
| Pinaceae | | | | |
| *Pinus* sp. 1 (Diploxylon type) | + | | | 2a |
| Asteraceae | | | | |
| *Artemisia* sp. 2 | + | | | 1a |
| Asteraceae gen. et spec. indet. 1 | + | | | 1a |
| Asteraceae gen. et spec. indet. 4 | + | | | 1a |
| Asteraceae gen. et spec. indet. 8 | + | | | 1a |
| Asteraceae gen. et spec. indet. 9 | + | | | 1a |
| Asteraceae gen. et spec. indet. 10 | + | | | 1a |
| Betulaceae | | | | |
| *Alnus* sp. 3 | + | | | 1a, 2a |
| *Betula* sp. | + | | | 1a |
| Caryophyllaceae | | | | |
| Caryophyllaceae gen. et spec. indet. 6 | + | | | 1b |
| Caryophyllaceae gen. et spec. indet. 8 | + | | | 1b |
| Caryophyllaceae gen. et spec. indet. 9 | + | | | 1b |
| Empetraceae | | | | |
| *Empetrum nigrum* | | + | | 1b |
| Ericaceae | | | | |
| *Vaccinium* cf. *uliginosum* | | + | | 1b |
| Ericaceae gen. et spec. indet. 6 | + | | | 1b |
| Euphorbiaceae | | | | |
| *Mercurialis perennis* | + | | | 1b |
| Onagraceae | | | | |
| Onagraceae gen. et spec. indet. | + | | | 1a |
| Plantaginaceae | | | | |
| *Plantago coronopus* | + | | | 1b |
| Poaceae | | | | |
| Poaceae gen. et spec. indet. 1 | + | | | 1b, 2a |
| Poaceae gen. et spec. indet. 4 | + | | | 1b, 2a |
| Poales | | | | |
| Poales gen. et spec. indet. | | + | | 1b, 2a |
| Polygonaceae | | | | |
| *Polygonum aviculare* | + | | | 1b |
| *Polygonum viviparum* | + | + | | 1b |
| *Rumex* sp. | + | | | 1b |

(continued)

**Table 11.4** (continued)

| Búlandshöfði Formation 1.1 Ma<br>Taxa | Pollen | Leaves | RP | DM |
|---|---|---|---|---|
| Ranunculaceae | | | | |
| Ranunculaceae gen. et spec. indet. 2 | + | | | 1b |
| Rosaceae | | | | |
| *Potentilla* sp. A | + | + | | ? |
| Salicaceae | | | | |
| *Salix* sp. B (*S. arctica* type) | (+)2 | + | (+) | 1a |
| *Salix herbacea* | (+)2 | + | (+) | 1a |
| Valerianaceae | | | | |
| *Valeriana* sp. | | + | | 1a |
| Incertae sedis – Magnoliophyta | | | | |
| Monocotyledonae fam. et gen. indet. 2 | + | | | ? |
| Pollen type 28 | + | | | ? |
| Pollen type 31 | + | | | ? |

*RP* reproductive structure, *DM* dispersal mode, *L* leafy axis, *A* fruit attached to leafy axis, *D* fruit dispersed, + organ included in a particular taxon, (+) organ belonging to genus but uncertain to which of the species, (+)2 indicating number of pollen types possibly belonging to the eponymous morphotaxon, *1a* wind long distance (anemochory), *1b* bird long distance (endozoochory), *2a* wind short distance (anemochory), *2b* animals short distance (exozoochory), *3* dyschory

The vegetation during the Stöð interglacial (marine isotope stage 31, Gibbard and Cohen 2009) was similar to the one described above from the Bakkabrúnir locality (cf. Table 11.3 vs. 11.5). One difference with the 1.7 Ma floral assemblage appears to be the better representation of coastal vegetation in the 1.1 Stöð flora. Onagraceae, *Plantago coronopus*, various Asteraceae, Polygonaceae and Poaceae may have been typical elements of sandy coastal vegetation on salt-rich soils (Fig. 11.11).

### *11.3.4 Svínafellsfjall Formation, Svínafell (0.8 Ma)*

The flora recovered from the lake sediments at Svínafell comprises 42 taxa, of which most are herbaceous angiosperms (24 taxa). Woody angiosperms consist of nine taxa, while conifers are represented by a single taxon (*Pinus*). Ferns and fern allies comprise seven taxa (Fig. 11.12; Plates 11.31–11.47). Except for the fern *Thelypteris limbosperma* (Bellardi ex All.) H. P. Fuchs, *Pinus* and *Alnus viridis*, all taxa encountered at Svínafell are part of the modern flora of Iceland (Table 11.6). Despite the closeness of the lake to a glacier (see Sect. 11.2.4), the vegetation in the vicinity of the lake appears to have been quite diverse (Table 11.7 and Fig. 11.13). Forest tundra with *Alnus*, *Betula* and *Sorbus aucuparia* in the canopy layer and *Salix* species and Ericaceae in the understorey may have been restricted to sheltered valleys, while shrublands and meadows thrived around the lake.

**Table 11.5** Vegetation types during the interglacial ca 1.1 Ma

| Vegetation types at the Stöð locality | | |
|---|---|---|
| **Swamp vegetation** | *Empetrum nigrum* | Lycopodiaceae gen. et spec. indet. 2 |
| *Osmunda* sp. | cf. *Vaccinium vitis-idaea* | Polypodiaceae gen. et spec. indet. 1 |
| *Alnus* sp. 3 | *Vaccinium uliginosum* | *Pinus* sp. 1 |
| Poaceae gen. et spec. indet. 1, 4 | Ericaceae gen. et spec. indet. 6 | *Alnus* sp. 3 |
| Poales gen. et spec. indet. | *Mercurialis perennis* | *Betula* sp. |
| | Poaceae gen. et spec. indet. 1, 4 | *Empetrum nigrum* |
| **Wet shrublands** | *Polygonum viviparum* | cf. *Vaccinium vitis-idaea* |
| Polypodiaceae gen. et spec. indet. 1 | Ranunculaceae gen. et spec. indet. 2 | *Vaccinium uliginosum* |
| Asteraceae gen. et. spec. indet. 1, 4, 8, 9, 10 | *Salix* sp. B (*S. arctica*) | Ericaceae gen. et spec. indet. 6 |
| *Alnus* sp. 3 | *Valeriana* sp. | *Mercurialis perennis* |
| *Betula* sp. | | *Salix herbacea* |
| *Mercurialis perennis* | **Coastal vegetation** | |
| Onagraceae gen. et spec. indet. | Onagraceae gen. et spec. indet. | **Rocky outcrop forest** |
| *Rumex* sp. | *Plantago coronopus* | *Lycopodium* sp. |
| Ranunculaceae gen. et spec. indet. 2 | *Mercurialis perennis* | *Huperzia* sp. |
| *Valeriana* sp. | *Artemisia* sp. 2 | *Pinus* sp. 1 |
| | Asteraceae gen. et spec. indet. 1, 4, 8, 9, 10 | *Empetrum nigrum* |
| **Meadows and shrublands** | Poaceae gen. et spec. indet. 1, 4 | cf. *Vaccinium vitis-idaea* |
| *Lycopodium* sp. | *Polygonum aviculare* | *Vaccinium uliginosum* |
| *Huperzia* sp. | *Rumex* sp. | Onagraceae gen. et spec. indet. |
| Lycopodiaceae gen. et spec. indet. 2 | *Potentilla* sp. A | *Plantago coronopus* |
| Polypodiaceae gen. et spec. indet. 1 | *Salix* sp. B (*S. arctica*) | *Polygonum aviculare* |
| *Artemisia* sp. 2 | | *Potentilla* sp. A |
| Asteraceae gen. et spec. indet. 1, 4, 8, 9, 10 | **Forest tundra** | *Salix* sp. B (*S. arctica*) |
| *Alnus* sp. 3 | *Lycopodium* sp. | *Salix herbacea* |
| Caryophyllaceae gen. et spec. indet. 6, 8, 9, 10 | *Huperzia* sp. | |

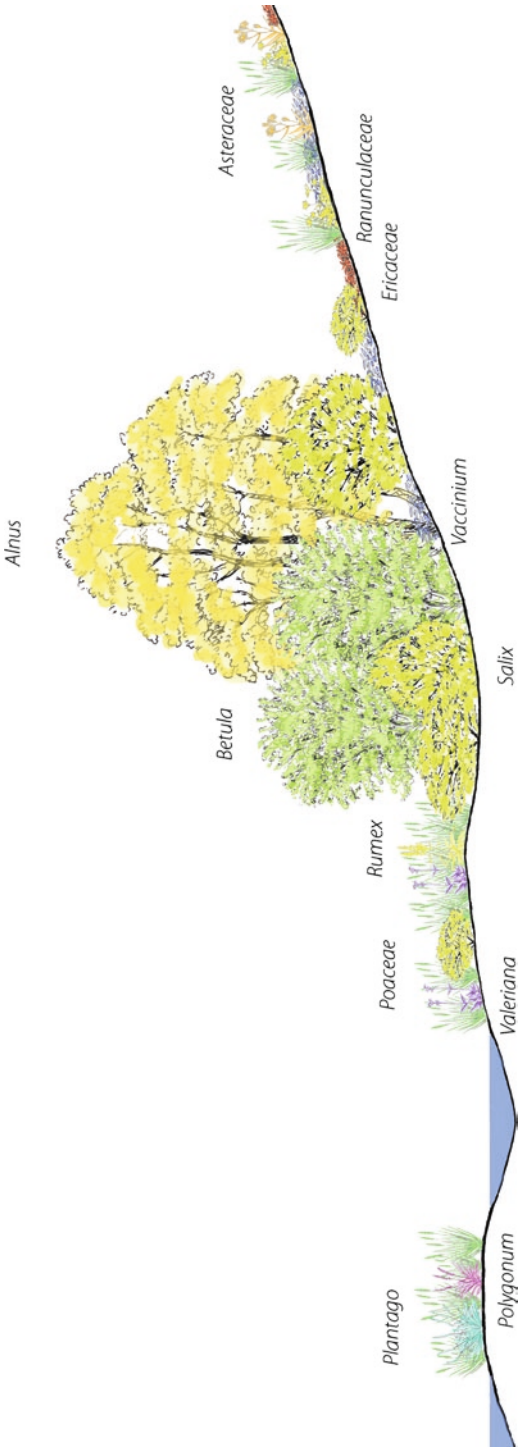



**Fig. 11.11** Schematic transect of coastal vegetation, meadows and forest tundra, 1.1 Ma in Iceland

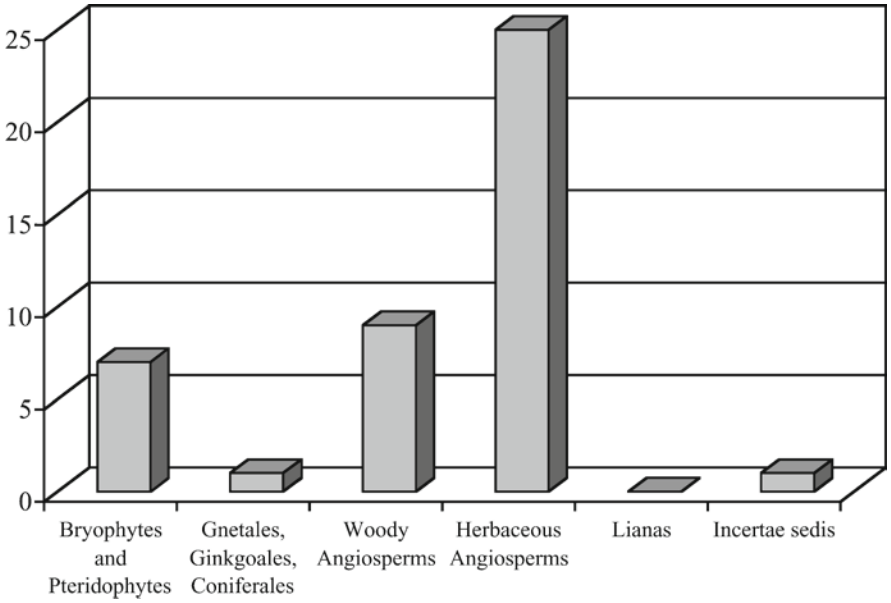



**Fig. 11.12** Distribution of life forms and higher taxa among the plants from the 0.8 Ma formation. Height of columns indicates number of taxa

**Table 11.6** Taxa recorded for the 0.8 Ma Svínafell flora

| Svínafellsfjall Formation 0.8 Ma<br>Taxa | Pollen | Leaves | RP | Other | DM |
|---|---|---|---|---|---|
| Bryophytes | | | | | |
| *Sphagnum* sp. | + | | | | 1a |
| Equisetaceae | | | | | |
| *Equisetum* sp. | | | | + | 1a |
| Lycopodiaceae | | | | | |
| *Lycopodium* sp. | + | | | | 1a |
| Polypodiaceae | | | | | |
| Polypodiaceae gen. et spec. indet. 1 | + | | | | 1a |
| Polypodiaceae gen. et spec. indet. A | | + | | | 1a |
| Thelipteridaceae | | | | | |
| *Thelipteris limbosperma* | | + | | | 1a |
| Incertae sedis – unassigned spores | | | | | |
| Trilete spore, fam., gen. et spec. indet. 9 | + | | | | 1a |
| Pinaceae | | | | | |
| *Pinus* sp. 1 (Diploxylon type) | + | | | | 2a |
| Apiaceae | | | | | |
| Apiaceae gen. et spec. indet. 10 | + | | | | 1b |
| Asteraceae | | | | | |
| *Artemisia* sp. 2 | + | | | | 1a |
| *Artemisia* sp. 3 | + | | | | 1a |
| Asteraceae gen. et spec. indet. 3 | + | | | | 1a |
| Asteraceae gen. et spec. indet. 4 | + | | | | 1a |
| Asteraceae gen. et spec. indet. 8 | + | | | | 1a |

(continued)

**Table 11.6** (continued)

| Svínafellsfjall Formation 0.8 Ma<br>Taxa | Pollen | Leaves | RP | Other | DM |
|---|---|---|---|---|---|
| Asteraceae gen. et spec. indet. 11 | + | | | | 1a |
| Asteraceae gen. et spec. indet. 12 | + | | | | 1a |
| Betulaceae | | | | | |
| *Alnus* cf. *viridis* | + | + | + D | | 1a |
| *Betula* sp. | + | | | | 1a |
| Chenopodiaceae | | | | | |
| Chenopodiaceae gen. et spec. indet. 3 | + | | | | 1b |
| Cyperaceae | | | | | |
| Cyperaceae gen. et spec. indet. C | | + | | | 1b |
| Ericaceae | | | | | |
| *Vaccinium* cf. *uliginosum* | | + | | | 1b |
| Ericaceae gen. et spec. indet. 6 | + | | | | 1b |
| Ericaceae gen. et spec. indet. 9 | + | | | | 1b |
| Menyanthaceae | | | | | |
| *Menyanthes* sp. | + | | | | 1b |
| Poaceae | | | | | |
| Poaceae gen. et spec. indet. 4 | + | | | | 1b, 2a |
| Poaceae gen. et spec. indet. 5 | + | | | | 1b, 2a |
| Poaceae gen. et spec. indet. 6 | + | | | | 1b, 2a |
| Poaceae gen. et spec. indet. 7 | + | | | | 1b, 2a |
| Poales | | | | | |
| Poales fam. gen. et spec. indet. | | + | | | 1b, 2a |
| Polygonaceae | | | | | |
| *Polygonum viviparum* | + | + | | | 1b |
| *Rumex* sp. | + | | | | 1b |
| Ranunculaceae | | | | | |
| *Thalictrum* sp. 2 | + | | | | 1b, 2a |
| Ranunculaceae gen. et spec. indet. 7 | + | | | | 1b |
| *Ranunculus* sp. A | | + | | | 1b |
| Rosaceae | | | | | |
| *Alchemilla* sp. | | + | | | 1b |
| *Dryas octopetala* | | + | | | 1a |
| *Sorbus* aff. *aucuparia* | | + | | | 1b |
| Rubiaceae | | | | | |
| *Galium* sp. | + | | | | 1b |
| Salicaceae | | | | | |
| *Salix* sp. B (*S. arctica* type) | (+) 3 | + | | | 1a |
| *Salix herbacea* | (+) 3 | + | | | 1a |
| Scrophulariaceae | | | | | |
| Scrophulariaceae gen. et. spec. indet. | + | | | | 1b |
| Incertae sedis – Magnoliophyta | | | | | |
| Pollen type 32 | + | | | | ? |

*RP* reproductive structure, *DM* dispersal mode, *L* leafy axis, *A* fruit attached to leafy axis, *D* fruit dispersed, + organ included in a particular taxon, (+) organ belonging to genus but uncertain to which of the species, (+)*2* indicating number of pollen types possibly belonging to the eponymous morphotaxon, *1a* wind long distance (anemochory), *1b* bird long distance (endozoochory), *2a* wind short distance (anemochory), *2b* animals short distance (exozoochory), *3* dyschory

**Table 11.7** Vegetation types during the interglacial ca 0.8 Ma (MIS 19)

Vegetation types at the Svínafell locality

**Swamp vegetation**
- *Sphagnum* sp.
- Apiaceae gen. et spec. indet. 10
- Cyperaceae gen. et spec. indet.
- Ericaceae gen. et spec. indet. 6, 9
- *Menyanthes* sp.
- Poales gen. et spec. indet.

**Wet shrublands**
- Polypodiaceae gen. et spec, indet. 1, A
- *Thelypteris limbosperma*
- Apiaceae gen. et spec. indet. 10
- *Betula* sp.
- *Alnus viridis*
- Cyperaceae gen. et spec. indet.
- *Rumex* sp.
- *Alchemilla vulgaris* type
- Scrophulariaceae gen. et spec. indet.

**Meadows and shrublands**
- *Sphagnum* sp.
- *Equisetum* sp.
- *Lycopodium* sp.
- Apiaceae gen. et spec. indet. 10
- *Artemisia* sp. 2, 3
- Asteraceae gen. et spec. indet. 3,4, 8, 11, 12
- *Betula* sp.
- Chenopodiaceae gen. et spec. indet. 3
- *Vaccinium uliginosum*
- Ericaceae gen. et spec. indet. 6, 9
- Poaceae gen. et spec, indet. 4, 5, 6, 7
- *Polygonum viviparum*
- *Thalictrum* sp. 2
- Ranunculaceae gen. et spec. indet. 7
- *Ranunculus* sp. A
- *Alchemilla vulgaris* type
- *Dryas octopetala*
- *Galium* sp.
- *Salix arctica/glauca*
- *Salix herbacea*
- *Salix* sp.
- Scrophulariaceae gen. et spec. indet.

**Coastal vegetation**
- *Equisetum* sp.
- Apiaceae gen. et spec. indet. 10
- *Artemisia* sp. 2, 3
- Asteraceae gen. et spec. indet. 3, 4, 8, 11,12
- Chenopodiaceae gen. et spec. indet. 3
- Cyperaceae gen. et spec. indet.
- Poaceae gen. et spec. indet. 4, 5, 6, 7
- *Rumex* sp.
- *Sorbus aucuparia*

**Forest tundra**
- Polypodiaceae gen. et spec. indet.
- *Thelypteris limbosperma*
- *Pinus* sp. 1
- *Alnus viridis*
- *Betula* sp.
- *Vaccinium uliginosum*
- Ericaceae gen. et spec. indet. 6, 9
- *Sorbus aucuparia*
- *Salix arctica/glauca*
- *Salix* sp.

**Rocky outcrop forest**
- *Lycopodium* sp.
- *Pinus* sp. 1
- Ericaceae gen. et spec. indet. 6, 9
- Poaceae gen. et spec. indet. 4, 5, 6, 7
- *Thalictrum* sp. 2
- Ranunculaceae gen. et spec. indet. 7
- *Sorbus aucuparia*
- *Galium* sp.
- *Salix herbacea*

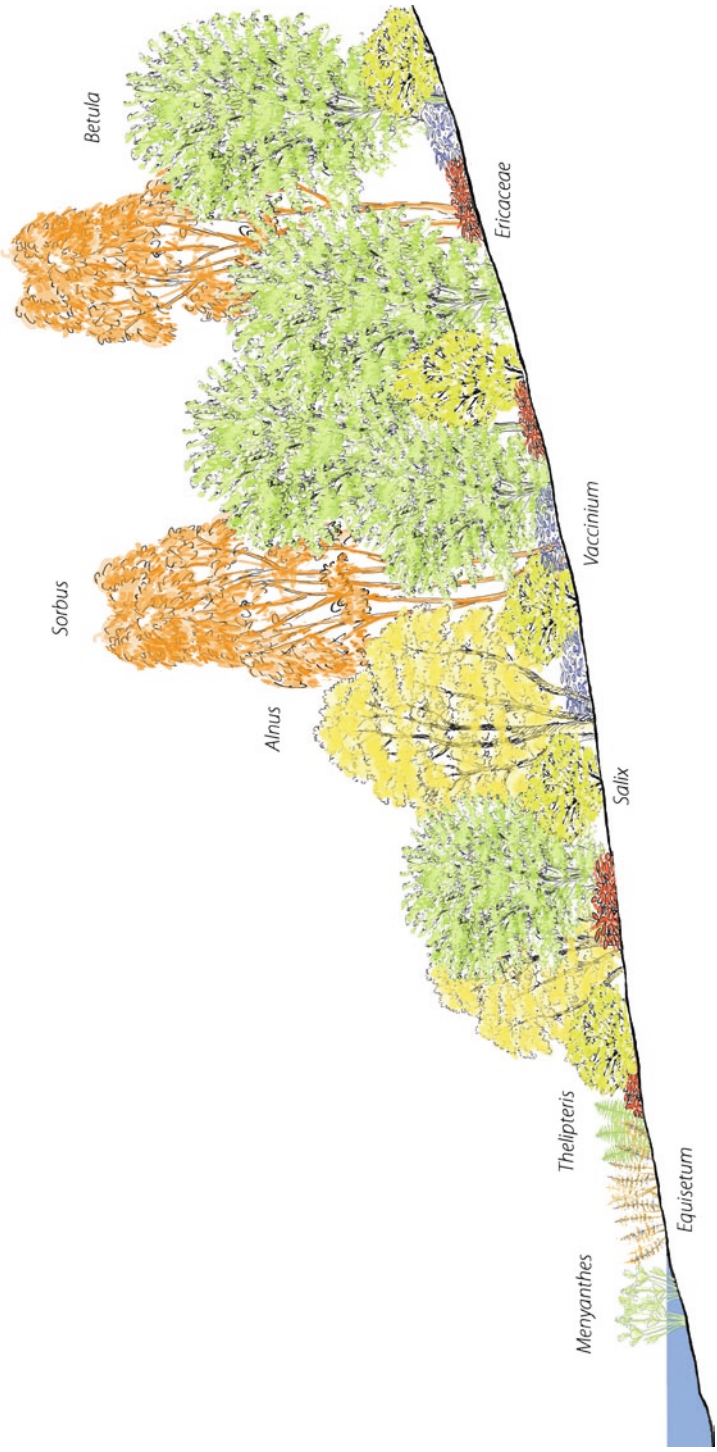



**Fig. 11.13** Schematic transect of forest tundra, 0.8 Ma in Iceland

## 11.4 Comparison to Coeval Northern Hemispheric Floras and Faunas

### *11.4.1 Subarctic and Arctic Floras*

A number of Pleistocene localities from Arctic areas in the northern hemisphere are well-documented. The Early Pleistocene (2.4 Ma) Kap København Formation in northern Greenland (82° 30' N) yielded a rich plant and animal record that witnessed a markedly warmer climate at these high latitudes during the Pleistocene than today (Bennike 1990; Funder et al. 2001). The northern part of Greenland today experiences a cold Polar tundra climate (ET; Fig. 11.14, 4; Nord), and further inland a Polar frost climate (EF) with $T_{max}$ below 0°C (Kottek et al. 2006). The Early Pleistocene vegetation of northern Greenland most likely was a boreal forest of *Larix*, *Picea*, *Thuja* and *Taxus* with *Alnus*, *Betula*, *Viburnum edule* (Michx.) Raf. and various small shrubs of Ericaceae and *Salix* in the understorey. Open shrublands were rich in herbaceous species (Appendix 11.1). At present, the most cold-resistant species of *Taxus*, *Taxus canadiensis* Marshall grows at MAT −5.1–13°C (Thompson et al. 1999) and at its northern range limit (almost 30° more to the south than in the Early Pleistocene) thrives under a Dfc climate (see Fig. 11.14, 3: Goose Bay).

Bennike (1990) estimated that during the deposition of the Kap København Formation the summer temperatures in northern Greenland were 7–8°C warmer than at present. This would also mean that no Inland Ice existed at this time. In addition, Bennike (1990) found that the warming relative to present was most pronounced at high latitudes. The same has been suggested based on sea surface temperature (SST) estimates for the Late Pliocene (3.3–3 Ma). Estimated SST from the drill cores of the Iceland Plateau were 11.7°C warmer than today, whereas those from the Arctic Ocean north of Svalbard were 18.1°C warmer (Robinson 2009). These temperature anomalies can be attributed to the much reduced albedo of Greenland and the Arctic Ocean when large parts are seasonally ice-free.

Matthews and Ovenden (1990) described Late Pliocene and Pleistocene plants from subarctic and Arctic northern America. The Niguanak Flora (69°N), Northern Alaska, was assigned an age of 2.7–2.5 Ma based on preliminary biostratigraphic correlation. This flora yielded one of the richest moss floras known from the Arctic. The moss flora is identical to the modern flora of northern Alaska. In contrast, the vascular plants contain a number of exotic taxa (*Larix*, *Picea*, *Pinus* subgenus *Strobus*; Appendix 11.1). Based on the insect and angiosperm remains an open character of the vegetation was suggested. Another locality, Ch'ijee's Bluff, unit two (67°N), Yukon, is probably of similar age (ca 2.5–2.1 Ma; Matthews and Ovenden 1990). *Abies*, *Larix*, *Picea* and *Pinus* section *Strobus* indicate the presence of forest tundra with an admixture of *Alnus* and *Betula* (Appendix 11.1). Ericaceae, *Myrica* (*M. gale* type) and *Cornus canadensis* L. were elements of the understorey. Although *Abies* currently does not distribute in Alaska and has a more southern distribution in Yukon (Thompson et al. 1999) the floral assemblage does not point

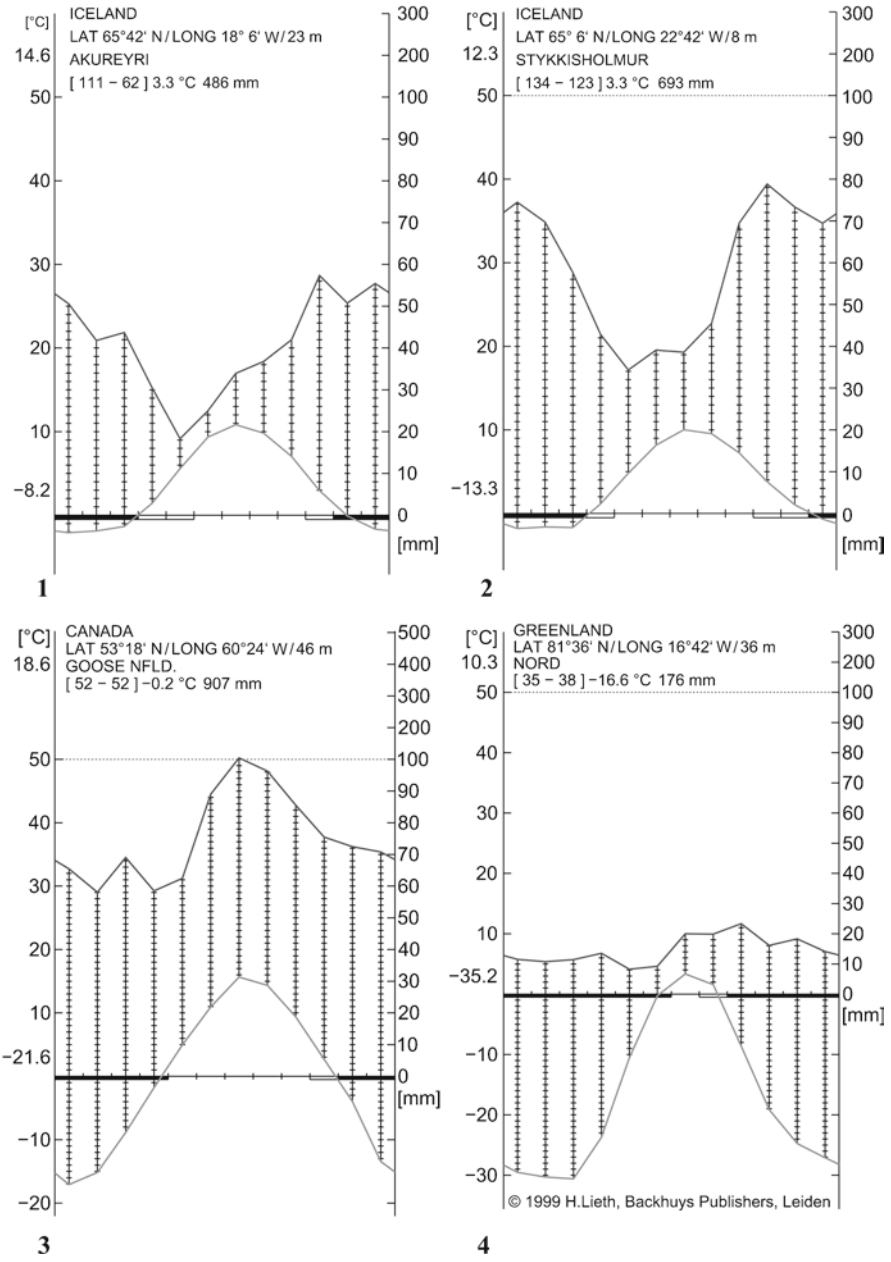



**Fig. 11.14** Climate diagrams for modern Iceland, Canada and Greenland (climate diagrams from Lieth et al. 1999). **1** Akureyri, Csc climate. **2** Stykkishólmur, Cfc climate. **3** Goose, Dfc climate. **4** Nord, ET climate (Climate types according to Köppen, cf. Kottek et al. 2006)

to a climate that is warmer than at present to the degree it has been inferred for the northern part of Greenland (see above).

The Lost Chicken locality (64°N), interior Alaska, has been well dated at ca 2.1 Ma. Based on the abundant occurrence of leaf fragments of *Larix* the palaeoenvironment at this site was *Larix* woodland surrounded by upland forests containing *Picea* and *Pinus* (Matthews and Ovenden 1990; Appendix 11.1). Based on their leaf anatomy, needles of *Pinus* represent a Eurasian type belonging to *Pinus* subsection *Cembrae*. This type persisted in subarctic and Arctic North America from the Late Miocene to ca 2 Ma; after this point, it disappeared from North America. Another element of the Lost Chicken flora, *Sambucus*, has been reported from various Late Tertiary sites in northern North America, whereas it has never been reported from Iceland. In Ellesmere Island, the flora from Wolf Valley is ca 1.5–1 Ma, similar in age to the floras of Bakkabrúnir and Stöð. Based on the absence of *Thuja* and *Pinus*, which are common in other, slightly older localities from the high-level alluvium in Ellesmere Island, and the presence of *Glyceria*, *Alnus viridis* subsp. *crispa* and *Nuphar* (Appendix 11.1), Matthews and Ovenden (1990) suggested that the climate was considerably warmer than today. *Glyceria*, *Alnus* and *Nuphar* do not grow at high latitudes in eastern North America at present (Meusel et al. 1965; Flora of North America Editorial Committee 1997).

Summing up, the Pleistocene floras described here are indicative of climates that were warmer than today with the strongest deviation from the present climate at the northernmost site (Kap København). Apart from this, a biogeographic pattern is seen in the floras. While taxa such as *Thuja* were present in Ellesmere Island, Meighen Island, and Prince Patrick Island 5–3 Ma (Matthews and Ovenden 1990), and at Kap København 2.4 Ma, they are not known from the floras of Iceland. This may suggest that a North American lineage of *Thuja* extended to the very northern tip of Greenland during the Pleistocene but never reached Iceland. *Larix* is present in a number of Pleistocene North American subarctic and Arctic localities (Appendix 11.1), whereas it disappears from Iceland after 3.8 Ma.

### *11.4.2 Northwestern Europe*

The vegetation and floral change across the Pliocene-Pleistocene boundary (ca 2.6 Ma) is well-documented in northwestern Europe. Pollen profiles and macrofossils suggest the presence of broadleaved deciduous forests with an admixture of conifers in the latest Pliocene (Piacenzian, Reuverian; Fig. 11.3). A number of taxa, typical of the European Neogene, persisted in these forests (for example, *Sequoia*, *Sciadopitys*, *Tsuga*, *Actinidia*, *Carya*, *Magnolia*, *Pterocarya*, *Eucommia*, *Nyssa*, *Liquidambar* and *Aesculus*; Lang 1994). Already in 1905, Clement and Eleanor Reid had studied seeds from the surroundings of the village Tegelen (Province

Limburg, Netherlands) (Reid and Reid 1907) and found that this (Pleistocene) flora contained 15% of exotic elements which in Europe were only known from the Tertiary. In clay beds near the town Reuver, south of Tegelen, they found that exotic species accounted for 50% of the flora and hence they concluded that the Reuver beds were older than the clay in the Tegelen clay pits (Hoek Ostende 2004). Since a first drop in the percentage of exotics occurs in Tegelen, the Reids assumed that the deposition of the Tegelen Clay must have been preceded by a glacial period. Based on the percentages of exotics, they defined stages, Reuverian for the older clay beds to the south and Teglian (=Tiglian) for the period in which the clay near Tegelen was deposited (Reid and Reid 1915; see Fig. 11.3). The border between these two stages corresponds roughly to the Pliocene-Pleistocene boundary as currently recognized (Gibbard and Cohen 2009).

Although the transition from the Pliocene to the Pleistocene in northwestern Europe is connected with the loss of exotic taxa, some occur again after the Praetiglian cold phase (for example, *Sciadopitys*, *Tsuga*, *Carya*, *Pterocarya*, *Eucommia*; Reid and Reid 1915; Lang 1994). This was probably connected to transient climate warming in the Tiglian (Early Pleistocene) as also seen in the Arctic floras (cf. Kap København Formation). By the Cromerian (ca 0.9–0.5 Ma) the flora in northwestern Europe was entirely void of exotic elements and very similar to the modern one (Reid and Reid 1915; Lang 1994).

## 11.5 Summary

Although all the Pleistocene floras in Iceland were deposited after the first major glaciations in the northern North Atlantic area (Eiríksson 2008), they may have thrived under quite different climatic conditions. The earliest Pleistocene (2.4 Ma) marked a time of global warmth. Based on fossil plants and insects, summer temperatures in northern Greenland probably were 7–8°C warmer than at present. This would also mean that no Inland Ice existed at this time. More data are needed from the 2.4 to 2.1 Ma Brekkukambur Formation of Iceland in order to evaluate whether and to which extent this temperature anomaly is also recorded in the plant fossil record of Iceland. The remaining plant-bearing Pleistocene formations of Iceland yield a rather homogeneous flora that is markedly similar to the modern flora and reflecting climatic and environmental conditions well-comparable to the modern ones. A small number of taxa that were present in the Pleistocene interglacials of Iceland are not found in Iceland today. Most prominent, *Alnus viridis* is represented by pollen and leaf fossils throughout the Pleistocene but absent from the modern flora. A likely explanation for the absence of this taxon from the modern flora of Iceland may be that its postglacial expansion was hindered by competition with other taxa rather than by climatic intolerance. The fact that the flora and vegetation of Iceland during interglacials remained virtually unchanged since at least 1.7 Ma, suggests that similar constraints acted on re-colonization of the island during large parts of the Pleistocene.

## Appendix 11.1

Floristic composition of the Pleistocene floras of Iceland compared to contemporaneous northern hemispheric fossil assemblages at high latitudes.

| **Pleistocene floras, Iceland**<br>**2.4–0.8 Ma**<br>This study | |
|---|---|
| 2 | Equisetum sp. |
| 1 | Huperzia sp. |
| 1 | Lycopodiaceae gen. et spec. indet. 2 |
| 1 | Lycopodium sp. |
| 1 | Osmunda sp. |
| 1 | Polypodiaceae gen. et spec. indet. 1 |
| 3 | Polypodiaceae gen. et spec. indet. A |
| 1 | Sphagnum sp. |
| 3 | Thelipteris limbosperma |
| 1 | Trilete spore, fam., gen. et spec. indet. 6 |
| 1 | Trilete spore, fam., gen. et spec. indet. 7 |
| 1 | Trilete spore, fam., gen. et spec. indet. 8 |
| 1 | Trilete spore, fam., gen. et spec. indet. 9 |
| 1 | Pinus sp. 1 (Diploxylon type) |
| 3 | Alchemilla sp. |
| 1-3 | Alnus aff. viridis |
| 1 | Alnus sp. 3 |
| 1 | Apiaceae gen. et spec. indet. 10 |
| 1 | Artemisia sp. 1 |
| 1 | Artemisia sp. 2 |
| 1 | Artemisia sp. 3 |
| 1 | Asteraceae gen. et spec. indet. 1 |
| 1 | Asteraceae gen. et spec. indet. 10 |
| 1 | Asteraceae gen. et spec. indet. 11 |
| 1 | Asteraceae gen. et spec. indet. 12 |
| 1 | Asteraceae gen. et spec. indet. 3 |
| 1 | Asteraceae gen. et spec. indet. 4 |
| 1 | Asteraceae gen. et spec. indet. 8 |
| 1 | Asteraceae gen. et spec. indet. 9 |
| 3 | Betula nana x pubescens |
| 1 | Betula sp. |
| 1 | Caryophyllaceae gen. et spec. indet. 5 |
| 1 | Caryophyllaceae gen. et spec. indet. 6 |
| 1 | Caryophyllaceae gen. et spec. indet. 7 |
| 1 | Caryophyllaceae gen. et spec. indet. 8 |
| 1 | Caryophyllaceae gen. et spec. indet. 9 |
| 1 | Chenopodiaceae gen. et spec. indet. 3 |
| 3 | Cyperaceae gen. et spec. indet. C |
| 3 | Dryas octopetala |
| 1 | Empetrum nigrum |
| 1 | Ericaceae gen. et spec. indet. 6 |
| 1 | Ericaceae gen. et spec. indet. 8 |
| 1 | Ericaceae gen. et spec. indet. 9 |
| 1 | Fragaria sp. |
| 1 | Galium sp. |
| 1 | Kobresia sp. |
| 1 | Menyanthes sp. |
| 1 | Mercurialis perennis |
| 1 | Monocotyledonae fam. et gen. indet. 2 |
| 1 | Myrica sp. |
| 1 | Onagraceae gen. et spec. indet. |
| 1 | Plantago coronopus |
| 1 | Poaceae gen. et spec. indet. 1 |
| 1 | Poaceae gen. et spec. indet. 4 |
| 1 | Poaceae gen. et spec. indet. 5 |
| 1 | Poaceae gen. et spec. indet. 6 |
| 1 | Poaceae gen. et spec. indet. 7 |
| 3 | Poales fam. gen. et spec. indet. |
| 1 | Pollen type 28 |
| 1 | Pollen type 31 |
| 1 | Pollen type 32 |
| 1 | Polygonum aviculare |
| 1 | Polygonum sect. Aconogonon sp. |
| 1, 3 | Polygonum viviparum |
| 1, 3 | Potentilla sp. A |
| 1 | Ranunculaceae gen. et spec. indet. 2 |
| 1 | Ranunculaceae gen. et spec. indet. 6 |
| 1 | Ranunculaceae gen. et spec. indet. 7 |
| 1 | Ranunculus sp. 3 |
| 3 | Ranunculus sp. A |
| 1 | Rosaceae gen. et spec. indet. 13 |
| 1 | Rumex sp. |
| 1, 3 | Salix herbacea |
| 1, 3 | Salix sp. B (S. arctica type) |
| 1 | Sanguisorba sp. |
| 1 | Saxifraga sp. |
| 1 | Scrophulariaceae gen. et spec. indet. |
| 3 | Sorbus aff. aucuparia |
| 1 | Thalictrum sp. 2 |
| 1 | Trollius sp. |
| 3 | Vaccinium cf. uliginosum |
| 3 | Valeriana sp. |

| **Kap København Formation, North Greenland [82°30´N] ca 2.4 Ma** (Bennike 1990; Funder et al. 2001) | | $B_1$ | $B_2$ | $B_3$ |
|---|---|---|---|---|
| 1 | Botrychium | | + | |
| 1 | Cystopteris sp. | + | + | |
| 1 | Gymnocarpium | + | + | |
| 1 | Huperzia | + | + | + |
| 2 | Equisetum sp. | + | + | + |
| 1,2 | Polypodiaceae | + | + | + |
| 1 | Selaginella selaginoides | | | + |
| 1 | Sphagnum | + | + | + |
| 1,2,3 | Larix groenlandii | | + | + |
| 1,2,3 | Picea mariana | + | + | + |
| 1 | Pinus | + | + | + |
| 3 | Taxus sp. | | | + |
| 2,3 | Thuja occidentalis | | | + |
| 1,2 | ?Arenaria sp. | | | + |
| 2 | ?Linaria sp. | | | + |
| 2 | ?Luzula sp. | | | + |
| 1,2,3 | **Alnus cf. crispa** | | + | + |
| 1,2,3 | Andromeda polifolia | | | + |
| 2 | Anemone sp. | | | + |
| 1,2 | Arabis cf. alpina | | + | + |
| 2 | Aracites globosa | | | + |
| 1 | Artemisia | + | + | + |
| 2 | Arctostaphylos uva-ursi | | | + |
| 1,2 | Betula alba s.1. | + | + | + |
| 1,2,3 | **Betula nana** | + | + | + |
| 1,2 | Carex cf. chordorrhiza | | | + |
| 1,2 | Carex spp. | + | + | + |
| 1,3 | Cassiope tetragona | | | + |
| 1,2 | Cerastium cf. arcticum/alpinum | | | + |
| 1 | Cirsium | | + | |
| 2 | Cornus canadensis [suffrutescent] | | | + |
| 2 | Cornus sp. A | | | + |
| 2 | Cornus stolonifera (syn. of C. sericea) | | | + |
| 1,2,3 | **Dryas octopetala** | + | + | + |
| 2,3 | **Empetrum nigrum s.1.** | + | + | + |
| 1 | Erigeron | | + | |
| 2 | Erodium sp. | | | + |
| 1 | Poaceae | + | + | + |
| 2 | Hedysarum sp. | | | + |
| 1,2 | Hippuris vulgaris | | + | + |
| 2 | Juncus sp. | | | + |
| 1,2 | Ledum palustre | | | + |
| 1,2 | **Melandrium affine/angustiflorum (syn. of Silene furcata)** | | | + |
| 1,2 | **Menyanthes trifoliata** | + | + | + |
| 1,2 | **Myrica arctogale** | + | + | + |

(continued)

| | | | | |
|---|---|---|---|---|
| **Kap København Formation** (continued) | | | | |
| 2 | Nuphar lutea | | | + |
| 1,3 | Oxycoccus palustris | + | | + |
| 1,2 | Oxyria digyna | + | + | + |
| 1,2 | Papaver sect. Scapiflora | + | + | + |
| 1,2 | **Polygonum sp. (viviparum)** | + | + | + |
| 1,2 | Potamogeton alpinus | | | + |
| 1,2 | Potamogeton cf. gramineus | | | + |
| 1,2 | Potamogeton cf. perfoliatus/richardsonii | | | + |
| 1,2 | Potamogeton cf. vaginatus | + | + | + |
| 1,2 | Potamogeton natans | + | + | + |
| 2 | **Potentilla palustris** | | | + |
| 1,2 | **Potentilla spp.** | + | + | + |
| 1,2 | **Ranunculus cf. pallasii** | + | + | + |
| 1,2 | **Ranunculus hyperboreus** | + | + | + |
| 2 | Rubus arcticus/saxatilis | | | + |
| 2 | Rubus chamaemorus | | | + |
| 2 | **Rumex acetosa** | + | | + |
| 1,3 | **Salix reticulata** | + | + | + |
| 1,2,3 | **Salix spp.** | + | + | + |
| 1 | Saxifraga sp. | + | + | + |
| 1,2 | Scirpus microcarpus | ? | ? | ? |
| 1 | Scrophulariaceae | | | + |
| 2 | Sedum annuum | | | + |
| 2 | Sparganium angustifolium | | | + |
| 1,2 | Stellaria sp. | | | + |
| 1,3 | **Vaccinium uliginosum var. microphyllum** | | + | + |
| 2 | Viburnum cf. edule | | | + |
| 2 | Viola sp. | | | + |

**Niguanak, Alaska [69°49'N, 143°05'W]**
**ca 2.7–2.5 Ma**
Matthews and Ovenden 1990

| | |
|---|---|
| 2 | **Equisetum sp.** |
| 2 | Abies sp. |
| 2 | Larix sp. |
| 2 | Picea sp. |
| 2 | Pinus subsect. Eustrobi (5-needled) |
| 2 | **Alnus sp.** |
| 2 | Andromeda polifolia |
| 2 | Arctostaphylos alpina/rubra type |
| 2 | Betula arboreal type |
| 2 | **Betula glandulosa type** |
| 2 | Caltha sp. |
| 2 | Carex spp. |
| 2 | Chamaedaphne sp. |
| 2 | Chrysosplenium sp. |
| 2 | **Dryas sp.** |
| 2 | **Empetrum nigrum** |
| 2 | Eriophorum sp. |
| 2 | Hippuris sp. |
| 2 | Lonicera sp. |
| 2 | **Menyanthes small type** |
| 2 | **Menyanthes trifoliata** |
| 2 | Populus sp. |
| 2 | Potamogeton richardsonii |
| 2 | Potamogeton spp. |
| 2 | **Potentilla norvegica** |
| 2 | **Potentilla sp.** |
| 2 | **Ranunculus hyperboreus** |
| 2 | **Ranunculus lapponicus** |
| 2 | Rosa sp. |

(continued)

| | **Niguanak, Alaska** (continued) |
|---|---|
| 2 | **Salix sp.** |
| 2 | Stellaria sp |
| 2 | **Vaccinium sp.** |
| 2 | Viola sp. |

| | **Wolf Valley, Ellesmere Island [~79°40'N, 82°W]ca 1–1.5 Ma** Matthews and Ovenden 1990 |
|---|---|
| 2 | **Equisetum sp.** |
| 2 | Larix sp. |
| 2 | Picea sp. |
| 2 | **Alnus crispa** |
| 2 | Andromeda polifolia |
| 2 | Betula arboreal type |
| 2 | **Betula dwarf shrub** |
| 2 | Caltha type |
| 2 | Carex spp. |
| 2 | **Caryophyllaceae gen. et spec. indet.** |
| 2 | **Chenopodium sp.** |
| 2 | **Dryas sp.** |
| 2 | Eriophorum sp. |
| 2 | Glyceria sp. |
| 2 | Hippuris sp. |
| 2 | Melandrium sp. (=Silene sp.) |
| 2 | **Menyanthes small type** |
| 2 | **Menyanthes trifoliata** |
| 2 | Nuphar sp. |
| 2 | Potamogeton spp. |
| 2 | **Potentilla palustris** |
| 2 | **Potentilla sp.** |
| 2 | **Ranunculus hyperboreus** |
| 2 | Sparganium hyperboreum |

| | **Ch'ijee's Bluff, unit 2, Yukon [67°28'N, 139°54'W] ca 2.5–2.1 Ma** Matthews and Ovenden 1990 |
|---|---|
| 2 | Abies sp. |
| 2 | Larix sp. |
| 2 | Picea sp. |
| 2 | Pinus 5-needled type undifferentiated |
| 2 | Pinus subsect. Eustrobi (5-needled) |
| 2 | Alisma sp. |
| 2 | **Alnus incana** |
| 2 | Andromeda sp. |
| 2 | Aracites globosa |
| 2 | Betula arboreal type |
| 2 | Carex aquatilis type |
| 2 | Carex rostrata type |
| 2 | Carex spp. |
| 2 | Chamaedaphne sp. |
| 2 | Cornus canadensis |
| 2 | **Dryas sp.** |
| 2 | Eliocharis sp. |
| 2 | **Empetrum nigrum** |
| 2 | Eriophorum sp. |
| 2 | Hippuris sp. |
| 2 | **Menyanthes small type** |
| 2 | **Menyanthes trifoliata** |
| 2 | **Myrica sp.** |
| 2 | Potamogeton sp. |
| 2 | **Potentilla palustris** |
| 2 | **Ranunculus hyperboreus** |
| 2 | **Ranunculus macounii/pensylvanicus type** |
| 2 | Rorippa islandica |
| 2 | **Salix sp.** |
| 2 | Sambucus sp. |
| 2 | Sparganium hyperboreum |

| | **Lost Chicken, interior Alaska [64°4.5'N, 141°54'W] ca 2.1 Ma** Matthews and Ovenden 1990 |
|---|---|
| 2 | Abies sp. |
| 2 | Larix sp. |
| 2 | Picea sp. |
| 2 | Pinus 5-needled type undifferentiated |
| 2 | Pinus subsect. Cembrae |
| 2 | Andromeda sp. |
| 2 | Aracites globosa |
| 2 | Carex spp. |
| 2 | Chamaedaphne sp. |
| 2 | Cicuta sp. |
| 2 | **Menyanthes trifoliata** |
| 2 | **Potentilla palustris** |
| 2 | **Potentilla sp.** |
| 2 | Sambucus sp. |

Boldface indicates that the genus is present in the Pleistocene of Iceland. Grey shading indicates that the genus is present in the older Pliocene Tjörnes beds. *1* based on pollen, spores; *2* based on leaves and/or fruit/seed fossils; *3* based on leaf fossils

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## Explanation of Plates

**Plate 11.1** Víðidalur Formation (Bakkabrúnir 1.7 Ma) **1–2**. Bakkabrúnir in Víðidalur, Víðidalur Formation (ca 1.7 Ma). **1**. The Bakkabrúnir outcrop. **2**. Detail showing the brownish and grayish lake sediments. **3–9**. Fossils are preserved in coarsely grained siltstones to fine grained sandstones. Most fossil are preserved as impressions only (**5**, **6**) but in some cases organic material is present (**3**, **4**)

**Plate 11.2** Víðidalur Formation (Bakkabrúnir 1.7 Ma) **1–3**. *Sphagnum* sp. **1**. Spore in SEM, proximal polar view. **2**. Detail of spore surface. **3**. Spore in LM, proximal polar view. **4–6**. *Lycopodium* sp. **4**. Spore in SEM, proximal polar view. **5**. Detail of spore surface. **6**. Spore in LM, polar view. **7–9**. *Lycopodium* sp. **7**. Spore in SEM, distal polar view. **8**. Detail of spore surface. **9**. Spore in LM, Polar view. **10–12**. *Huperzia* sp. **10**. Spore in SEM, equatorial view. **11**. Detail of spore surface. **12**. Spore in LM, proximal polar view

**Plate 11.3** Víðidalur Formation (Bakkabrúnir 1.7 Ma) **1–3**. *Osmunda* sp. **1**. Spore in SEM. **2**. Detail of spore surface. **3**. Spore in LM. **4–6**. Polypodiaceae gen. et spec. indet. 1. **4**. Spore in SEM, equatorial view. **5**. Detail of spore surface. **6**. Spore in LM. **7–9**. Trilete spore fam. gen. et spec. indet. 6. **7**. Spore in SEM, polar view. **8**. Detail of spore surface. **9**. Spore in LM, polar view. **10–12**. Trilete spore fam. gen. et spec. indet. 7. **10**. Spore in SEM, distal polar view. **11**. Detail of spore surface. **12**. Spore in LM, proximal polar view

**Plate 11.4** Víðidalur Formation (Bakkabrúnir 1.7 Ma) **1–3**. *Pinus* sp. 1 (Diploxylon type). **1**. Bisaccate pollen grain in SEM, proximal polar view. **2**. Detail showing boundary between corpus (*right*) and saccus (*left*). **3**. Bisaccate pollen grain in LM, distal polar view. **4–6**. *Pinus* sp. 1 (Diploxylon type). **4**. Bisaccate pollen grain in SEM, distal polar view. **5**. Detail of pollen grain surface showing both saccus (*upper left*) and corpus (*lower right*). **6**. Bisaccate pollen grain in LM, polar view. **7–9**. *Artemisia* sp. 1. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view. **10–12**. Asteraceae gen. et spec. indet. 1. **10**. Pollen grain in SEM, polar view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, polar view

**Plate 11.5** Víðidalur Formation (Bakkabrúnir 1.7 Ma) **1**. *Alnus* aff. *viridis*, small suborbiculate leaf (S 116551). **2**. Detail of Fig. 1 showing secondary venation and toothed margin. **3**. *Alnus* aff. *viridis*, small ovate leaf (S 116558). **4**. *Alnus* aff. *viridis*, fragment of lamina showing subsidiary venation. **5**. *Alnus* aff. *viridis*, large leaf (S 116546). **6**. *Betula nana* x *pubescens*, small ovate leaf (S). **7**. Detail of Fig. 6 showing marginal venation and teeth

**Plate 11.6** Víðidalur Formation (Bakkabrúnir 1.7 Ma) **1–3**. *Alnus* sp. 1. **1**. Pollen grain in SEM, polar view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, polar view. **4–6**. *Alnus* sp. 3. **4**. Pollen grain in SEM, polar view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, polar view. **7–9**. *Betula* sp. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, polar view. **10–12**. Caryophyllaceae gen. et spec. indet. 5. **10**. Pollen grain in SEM. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM

**Plate 11.7** Víðidalur Formation (Bakkabrúnir 1.7 Ma) **1**. *Vaccinium* cf. *uliginosum*, small elliptic leaf (S 116555). **2**. *Vaccinium* cf. *uliginosum*, small suborbiculate leaf (S 116554). **3**. *Polygonum viviparum*, elliptic leaf (S 116547). **4**. *Dryas octopetala*, small ovate leaf (S). **5**. *Salix* sp. B (*S. arctica* type), medium sized elliptic leaf, acute base (S 116557). **6**. *Salix* sp. B (*S. arctica* type), medium sized wide elliptic leaf (S 116545). **7**. Detail of Fig. 6 showing secondary and tertiary venation, and entire margin. **8**. *Salix* sp. B (*S. arctica* type), small elliptic leaf, round obtuse base (S 116548). **9**. Detail of Fig. 8 showing secondary and tertiary venation

**Plate 11.8** Víðidalur Formation (Bakkabrúnir 1.7 Ma) **1–3**. Caryophyllaceae gen. et spec. indet. 6. **1**. Pollen grain in SEM. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM. **4–6**. Caryophyllaceae gen. et spec. indet. 7. **4**. Pollen grain in SEM. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM. **7–9**. *Kobresia* sp. **7**. Pollen grain in SEM. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM. **10–12**. Ericaceae gen. et spec. indet. 8. **10**. Tetrad in SEM. **11**. Detail of pollen grain surface. **12**. Tetrad in LM

**Plate 11.9** Víðidalur Formation (Bakkabrúnir 1.7 Ma) **1–3**. *Menyanthes* sp. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4–6**. *Myrica* sp. **4**. Pollen grain in SEM, polar view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, polar view. **7–9**. *Myrica* sp. **7**. Pollen grain in SEM, polar view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, polar view

**Plate 11.10** Víðidalur Formation (Bakkabrúnir 1.7 Ma) **1–3**. *Polygonum viviparum*. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4–6**. *Rumex* sp. **4**. Pollen grain in SEM, polar view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, polar view. **7–9**. *Polygonum* sect. *Aconogonon* sp. **7**. Pollen grain in SEM. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM. **10–12**. *Ranunculus* sp. 3. **10**. Pollen grain in SEM, polar view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, polar view

**Plate 11.11** Víðidalur Formation (Bakkabrúnir 1.7 Ma) **1–3**. *Thalictrum* sp. 2. **1**. Pollen grain in SEM. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM. **4–6**. *Trollius* sp. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7–9**. Ranunculaceae gen. et spec. indet. 2. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view. **10–12**. Ranunculaceae gen. et spec. indet. 6. **10**. Pollen grain in SEM, equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, equatorial view

**Plate 11.12** Víðidalur Formation (Bakkabrúnir 1.7 Ma) **1–3**. *Fragaria* sp. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4–6**. *Fragaria* sp. 1. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7–9**. *Sanguisorba* sp. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view. **10–12**. Rosaceae gen. et spec. indet. 13. **10**. Pollen grain in SEM, equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, equatorial view

**Plate 11.13** Víðidalur Formation (Bakkabrúnir 1.7 Ma) **1–3**. *Salix* sp. 5. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM. **4–6**. *Salix* sp. 5. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7–9**. *Salix* sp. 5. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view. **10–12**. *Salix* sp. 6. **10**. Pollen grain in SEM, equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, equatorial view

**Plate 11.14** Víðidalur Formation (Bakkabrúnir 1.7 Ma) 1–**3**. *Saxifraga* sp. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4–6**. Pollen grain type 28. **4**. Pollen grain in SEM. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM. **7–9**. Pollen grain type 28. Pollen grain in SEM. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM. **10–12**. Pollen grain type 28. **10**. Pollen grain in SEM. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM

**Plate 11.15** Búlandshöfði Formation (Stöð 1.1 Ma) **1**. Stöð on Snæfellsnes, Búlandshöfði Formation (ca 1.1 Ma). **2**. Mt Kirkjufell and the surrounding lowland seen from the outcrop in Mt Stöð. **3**. Detail Mt Stöð where the outcrop is located. **4**. Thickness of the sedimentary unit at Stöð ranging from the lower right to the upper left corner of photo. **5**. Lagoon sediments overlain by deltaic sandstones. **6–9**. Plant remains are preserved in lagoon sediments, they occur mostly as impressions preserved in sandy siltstone

**Plate 11.16** Búlandshöfði Formation (Stöð 1.1 Ma) **1–3**. *Lycopodium* sp. **1**. Spore in SEM, oblique view. **2**. Detail of spore surface. **3**. Spore in LM, polar view. **4–6**. *Huperzia* sp. **4**. Spore in SEM, proximal polar view. **5**. Detail of spore surface. **6**. Spore in LM, polar view. **7–9**. Lycopodiaceae gen. et spec. indet. 2. **7**. Spore in SEM, proximal polar view. **8**. Detail of spore surface. **9**. Spore in LM, polar view. **10–12**. *Osmunda* sp. **10**. Spore in SEM. **11**. Detail of spore surface. **12**. Spore in LM

**Plate 11.17** Búlandshöfði Formation (Stöð 1.1 Ma) **1–3**. Polypodiaceae gen. et spec. indet. 1. **1**. Spore in SEM, equatorial view. **2**. Detail of spore surface. **3**. Pollen grain in LM, equatorial view. **4–6**. Trilete spore fam. gen. et spec. indet. 8. **4**. Spore in SEM. **5**. Detail of spore surface. **6**. Spore in LM. **7–9**. *Pinus* sp. 1 (Diploxylon type). **7**. Bisaccate pollen grain in SEM, proximal view. **8**. Detail of cappa surface. **9**. Pollen grain in LM, polar view. **10–12**. *Artemisia* sp. 2. **10**. Pollen grain in SEM, equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, equatorial view

**Plate 11.18** Búlandshöfði Formation (Stöð 1.1 Ma) **1–3**. Asteraceae gen. et spec. indet. 1 (aff. *Lapsana communis*). **1**. Pollen grain in SEM, polar view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, polar view. **4–6**. Asteraceae gen. et spec indet. 4. **4**. Pollen grain in SEM, polar view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, polar view. **7–9**. Asteraceae gen. et spec. indet. 4. **7**. Pollen grain in SEM, polar view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, polar view. **10–12**. Asteraceae gen. et spec. indet. 8. **10**. Pollen grain in SEM, oblique equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, equatorial view

**Plate 11.19** Búlandshöfði Formation (Stöð 1.1 Ma) **1–3**. Asteraceae gen. et spec. indet. 8. **1**. Pollen grain in SEM, polar view. 2. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4–6**. Asteraceae gen. et spec. indet. 9. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7–9**. Asteraceae gen. et spec. indet. 9. **7**. Pollen grain in SEM, polar view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, polar view. **10–12**. Asteraceae gen. et spec. indet. 10. **10**. Pollen grain in SEM, equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM

**Plate 11.20** Búlandshöfði Formation (Stöð 1.1 Ma) **1–3**. *Alnus* sp. 3. **1**. Pollen grain in SEM, polar view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, polar view. **4–6**. *Alnus* sp. 3. **4**. Pollen grain in SEM, polar view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, polar view. **7–9**. *Betula* sp. **7**. Pollen grain in SEM, polar view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, polar view. **10–12**. *Betula* sp. **10**. Pollen grain in SEM, polar view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, polar view

**Plate 11.21** Búlandshöfði Formation (Stöð 1.1 Ma) **1–3**. Caryophyllaceae gen. et spec. indet. 8. **1**. Pollen grain in SEM. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM. **4–6**. Caryophyllaceae gen. et spec. indet. 9. **4**. Pollen grain in SEM. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM. **7–9**. Caryophyllaceae gen. et spec. indet. 8. **7**. Pollen grain in SEM. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM. **10–12**. Caryophyllaceae gen. et spec. indet. 8. **10**. Pollen grain in SEM. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM

**Plate 11.22** Búlandshöfði Formation (Stöð 1.1 Ma) **1**. *Empetrum nigrum*, leafy axes (IMNH org 286-02). **2**. *Vaccinium* cf. *uliginosum*, small narrow obovate leaf (IMNH 404-01). **3**. *Vaccinium* cf. *uliginosum*, elliptic leaf (IMNH 6572). **4**. Poales gen. et spec. indet., part of leaf or axes. **5**. *Polygonum viviparum*, wide elliptic leaf with petiole (IMNH org 271). **6**. *Polygonum viviparum*, narrow elliptic leaf with a long petiole (IMNH org 285). **7**. *Polygonum viviparum*, small lorate leaf (S). **8**. *Polygonum viviparum*, detail showing secondary and higher ordered venation, veins branching towards margin (S)

**Plate 11.23** Búlandshöfði Formation (Stöð 1.1 Ma) **1–4**. Ericaceae gen. et spec. indet. 6. **1**. Tetrad in SEM. **2**. Detail of tetrad surface. **3**. Tetrad in LM. **4**. Detail of tetrad surface. **5–7**. *Mercurialis perennis*. **5**. Pollen grain in SEM, equatorial view. **6**. Detail of pollen grain surface. **7**. Pollen grain in LM, equatorial view. **8–10**. *Plantago coronopus*. **8**. Pollen grain in SEM. **9**. Detail of pollen grain surface. **10**. Pollen grain in LM

**Plate 11.24** Búlandshöfði Formation (Stöð 1.1 Ma) **1–4**. Onagraceae gen. et spec. indet. **1**. Pollen grain in SEM, proximal polar view. **2**. Detail of pollen grain surfaceshowing a long viscin thread. **3**. Detail of pollen grain surface. **4**. Pollen grain in LM, polar view. **5–7**. Poaceae gen. et spec. indet 1. **5**. Pollen grain in SEM. **6**. Detail of pollen grain surface. **7**. Pollen grain in LM. **8–10**. Poaceae gen. et spec. indet. 4. **8**. Pollen grain in SEM. **9**. Detail of pollen grain surface. **10**. Pollen grain in LM

**Plate 11.25** Búlandshöfði Formation (Stöð 1.1 Ma) **1–3**. *Polygonum aviculare*. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4–6**. *Polygonum viviparum*. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7–9**. *Rumex* sp. **7**. Pollen grain in SEM, polar view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM. **10–12**. Ranunculaceae gen. et spec. indet. 2. **10**. Pollen grain in SEM, polar view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM

**Plate 11.26** Búlandshöfði Formation (Stöð 1.1 Ma) **1–2**. *Potentilla* sp. A, small odd pinnately compound leaf (S 116552). Detail of Fig. 1 showing small leaflets. **3–5**. *Potentilla* sp. 2. **3**. Pollen grain in SEM, equatorial view. **4**. Detail of pollen grain surface. **5**. Pollen grain in LM, equatorial view. **6**. *Valeriana* sp., asymmetrical leaflet (IMNH org 274)

**Plate 11.27** Búlandshöfði Formation (Stöð 1.1 Ma) **1–2**. *Salix herbaceae* (116526). **1**. Suborbiculate leaf with petiole. **2**. Detail of Fig.1 showing venation and toothed margin. **3–10**. *Salix* sp. B (*S. arctica* type). **3**. Wide elliptic leaf (IMNH 399). **4**. Elliptic leaf (S). **5**. Detail of Fig. 4 showing secondary and higher ordered venation, and entire margin. **6**. Small elliptic leaf (IMNH org 270). **7**. Small obovate leaf (IMNH 403). **8**. Small elliptic leaf (IMNH 6918). **9**. Small elliptic leaf (IMNH 395). **10**. Large narrow obovate leaf (IMNH 393)

**Plate 11.28** Búlandshöfði Formation (Stöð 1.1 Ma) **1**. *Salix* sp., female catkins (IMNH 398-02). **2**. Detail of Fig. 1 showing open two-valved capsules. **3**. *Salix* sp., leafless branch (IMNH 399-02). **4**. *Salix* sp., leafless branch (IMNH 398-03)

**Plate 11.29** Búlandshöfði Formation (Stöð 1.1 Ma) **1–3**. *Salix* sp. 5. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4–6**. *Salix* sp. 7. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7–9**. Pollen grain type 28. **7**. Pollen grain in SEM. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM. **10–12**. Pollen grain type 31. **10**. Pollen grain in SEM. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM

**Plate 11.30** Svínafellsfjall Formation (Svínafell 0.8 Ma) **1**. Svínafellsfjall in Öræfi, Svínafellsfjall Formation (ca 0.8 Ma). **2**. The lake sediments of Svínafell. **3**. Typical outcrop with relatively thick lake sediments at Svínafell. **4**. Close-up showing the change from fine grained claystones and siltstones (grey) to sandy siltstones and sandstones (brown). **5**. Close-up showing the fine lamination in the fine grained rocks as well as small drop-stones. **6**. The erosive contact-zone between the brown lake sedimentary units and the more bluish glacial/fluvial sedimentary unit. **7**. Close-up of the glacial/fluvial sedimentary rock unit. **8**. Fossils are preserved in the fine grained siltstones in the lower part of the lake sedimentary unit

**Plate 11.31** Svínafellsfjall Formation (Svínafell 0.8 Ma) **1–3**. *Sphagnum* sp. **1**. Spore in SEM, proximal polar view. **2**. Detail of spore surface. **3**. Spore in LM, polar view. **4–6**. *Lycopodium* sp. **4**. Spore in SEM, distal polar view. **5**. Detail of spore surface. **6**. Spore in LM, polar view. **7–9**. Polypodiaceae gen. et spec. indet. 1. **7**. Spore in SEM, equatorial view. **8**. Detail of spore surface. **9**. Spore in LM, equatorial view. **10–12**. Trilete spore, fam., gen. et spec. indet. 9. **10**. Spore in SEM, proximal polar view. **11**. Detail of spore surface. **12**. Spore in LM, polar view

**Plate 11.32** Svínafellsfjall Formation (Svínafell 0.8 Ma) **1–2**. Polypodiaceae gen. et spec. indet A (IMNH 2927). **1**. Part of frond, pinnately compound. **2**. Detail of pinnae. **3–4**. *Thelypteris limbosperma* (S 116560). **3**. Detail of pinnulae, with single central vein and several pairs of lateral veins. **4**. Part of pinna, deeply lobed

**Plate 11.33** Svínafellsfjall Formation (Svínafell 0.8 Ma) **1–3**. *Pinus* sp. 1 (Diploxylon type). **1**. Bisaccate pollen grain grain in SEM, proximal view. **2**. Detail of saccus surface. **3**. Bisaccate pollen grain grain in LM, equatorial view. **4–6**. Apiaceae gen. et spec. indet. 10. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, Equatorial view. **7–9**. *Artemisia* sp. 3. **7**. Pollen grain grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view. **10–12**. *Artemisia* sp. 2. **10**. Pollen grain in SEM, polar view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, equatorial view (*left*), polar view (*right*)

**Plate 11.34** Svínafellsfjall Formation (Svínafell 0.8 Ma) **1–3**. Asteraceae gen. et. spec. indet. 3. **1**. Pollen grain in SEM, polar view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, polar view (*left*), equatorial view (*right*). **4–6**. Asteraceae gen. et spec. indet. 4. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain wall and surface. **6**. Pollen grain in LM, polar view. **7–9**. Asteraceae gen. et spec. indet. 8. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view (*left*), polar view right. **10–12**. Asteraceae gen. et spec. indet. 11. **10**. Pollen grain in SEM, equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, equatorial view

**Plate 11.35** Svínafellsfjall Formation (Svínafell 0.8 Ma) **1–3**. Asteraceae gen. et spec. indet. 12. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, oblique view (*left*), polar view (*right*). **4–6**. *Alnus* sp. 3. **4**. Pollen grain in SEM, polar view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, polar view. **7–9**. *Betula* sp. **7**. Pollen grain in SEM, polar view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, polar view. **10–12**. Chenopodiaceae gen. et spec. indet. 3. **10**. Pollen grain in SEM. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM

**Plate 11.36** Svínafellsfjall Formation (Svínafell 0.8 Ma) **1**–**6**. *Alnus* cf. *viridis*. **1**. Medium sized ovate leaf with fine teeth (IMNH org 51). **2**. Large elliptic leaf with large teeth (IMNH 2964). **3**. Leaf with several subsidiary veins (IMNH 2952). **4**. Small elliptic leaf with round base (IMNH 2919). **5**. Small leaf with cordate base (IMNH 2917). **6**. Detail of Fig. 1, showing apex and teeth

**Plate 11.37** Svínafellsfjall Formation (Svínafell 0.8 Ma) **1**–**7**. *Alnus* cf. *viridis*. **1**. Detail of margin, showing large teeth and marginal veins (IMNH 2964). **2**. Detail of apical margin, showing fine teeth (IMNH 2918). **3**. Detail of basal margin, showing subsidiary veins and teeth (IMNH org 51). **4**. Detail of lamina, showing tertiary venation (IMNH 2952). **5**. Detail of lamina, showing tertiary and higher ordered venation (IMNH 2969). **6**. Female strobili (IMNH 2975-03). **7**. Winged seed (IMNH 2967-04)

**Plate 11.38** Svínafellsfjall Formation (Svínafell 0.8 Ma) **1**–**3**. Ericaceae gen. et spec. indet. 6. **1**. Pollen tetrad in SEM. **2**. Detail of pollen tetrad surface. **3**. Pollen tetrad in LM. **4**–**6**. Ericaceae gen. et spec. indet. 9. **4**. Tetrad in SEM. **5**. Detail of tetrad surface. **6**. Tetrad in LM. **7**–**9**. *Menyanthes* sp. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view. **10**–**12**. *Menyanthes* sp. **10**. Pollen grain in SEM, equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, equatorial view

**Plate 11.39** Svínafellsfjall Formation (Svínafell 0.8 Ma) **1**. Cyperaceae gen. et spec. indet. C, part of leaf (IMNH 2915). **2**. *Vaccinium* cf. *uliginosum*, small brochidodromous leaf. **3**. Poales fam. gen. et spec. indet., fragment of leaf. **4**–**6**. *Polygonum viviparum*. **4**. Lower part of a lorate leaf (IMNH 5333-03). **5**. Elliptic leaf (IMNH org 56). **6**. Elliptic leaf, counterpart to 4 (IMNH 2938-01)

**Plate 11.40** Svínafellsfjall Formation (Svínafell 0.8 Ma) **1**–**3**. Poaceae gen. et spec. indet. 1 **1**. Pollen grain in SEM, oblique view. **2**. Detail of pollen surface. **3**. Pollen grain in LM, oblique view. **4**–**6**. Poaceae gen. et spec. indet. 4. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, oblique view. **7**–**9**. Poaceae gen. et spec. indet. 5. **7**. Pollen grain in SEM, polar view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, polar view. **10**–**12**. Poaceae gen. et spec. indet. 6. **10**. Pollen grain in SEM, polar view. **11**. Detail of Pollen grain surface. **12**. Pollen in LM, polar view

**Plate 11.41** Svínafellsfjall Formation (Svínafell 0.8 Ma) **1**–**3**. *Polygonum viviparum*. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain wall and surface. **3**. Pollen grain in LM, polar view. **4**–**6**. Rumex sp. **4**. Pollen grain in SEM, polar view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view (*left*), polar view (*right*). **7**–**9**. *Thalictrum* sp. 2. **7**. Pollen grain in SEM. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM

**Plate 11.42** Svínafellsfjall Formation (Svínafell 0.8 Ma) **1**–**4**. *Ranunculus* sp. A. **1**. Basal part of large leaf (IMNH 2942-01). **2**. Lobed leaf (IMNH 2940). **3**. Detail of Fig. 1, showing margin with large teeth. **4**. Detail of margin, showing marginal venation and large teeth (IMNH 2941)

**Plate 11.43** Svínafellsfjall Formation (Svínafell 0.8 Ma) **1**. *Ranunculus* sp. A, part of lobed lamina (IMNH 2943). **2**–**4**. *Alchemilla* sp. **2**. Medium sized lobed leaf (IMNH 2945). **3**. Detail of Fig. 2, showing secondary and higher ordered venation and toothed margin. **4**. Small leaf (IMNH 2944). **5**. *Dryas octopetala*, small leaf (IMNH 2942-02). **6**. *Sorbus* aff. *aucuparia*, pinnately compound leaf (IMNH 2951)

**Plate 11.44** Svínafellsfjall Formation (Svínafell 0.8 Ma) **1**–**3**. Ranunculaceae gen. et spec. indet. 7. **1**. Pollen grain in polar view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM. **4**–**6**. *Galium* sp. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view (*left*), polar view (*right*). **7**–**9**. *Salix* sp. 3. **7**. Pollen grain in SEM,

equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view. **10**–**12**. *Salix* sp. 5. **10**. Pollen grain in SEM, equatorial view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, equatorial view

**Plate 11.45** Svínafellsfjall Formation (Svínafell 0.8 Ma) **1**–**8**. *Salix* sp. B (*S. arctica* type). **1**. Medium sized elliptic leaf (IMNH org 55). **2**. Elliptic leaf (IMNH 2987). **3**. Large elliptic leaf (IMNH 2930). **4**. Detail of Fig. 1, showing secondary and tertiary venation. **5**. Detail of Fig. 3, showing entire margin and tertiary venation. **6**. Small narrow obovate leaf (IMNH 2909). **7**. Obovate medium sized leaf (IMNH org 57). **8**. Detail of Fig. 8, showing tertiary venation, marginal venation and entire margin

**Plate 11.46** Svínafellsfjall Formation (Svínafell 0.8 Ma) **1**–**6**. *Salix* sp. B (*S. arctica* type). **1**. Elliptic leaf (IMNH 2912). **2**. Detail of Fig. 1, showing secondary venation. **3**. Narrow elliptic leaf, acute apex (IMNH 2978-03). **4**. Large wide elliptic leaf (IMNH 2904). **5**. Detail of Fig. 4, showing part of lamina and venation. **6**. Small elliptic leaf (IMNH 2901). **7**–**10**. *Salix herbaceae*. **7**. Small orbiculate leaf with part of petiole preserved (S 116561). **8**. Small suborbiculate leaf (IMNH org 54). **9**. Detail of Fig. 7, showing lateral marginal venation and teeth. **10**. Detail of Fig. 7, showing apex of leaf

**Plate 11.47** Svínafellsfjall Formation (Svínafell 0.8 Ma) **1**–**3**. *Salix* sp. 8. **1**. Pollen grain in SEM, equatorial view. **2**. Detail of pollen grain surface. **3**. Pollen grain in LM, equatorial view. **4**–**6**. *Salix* sp. 8. **4**. Pollen grain in SEM, equatorial view. **5**. Detail of pollen grain surface. **6**. Pollen grain in LM, equatorial view. **7**–**9**. Scrophulariaceae gen. et spec. indet. **7**. Pollen grain in SEM, equatorial view. **8**. Detail of pollen grain surface. **9**. Pollen grain in LM, equatorial view (*left*), polar view (*right*). **10**–**12**. Pollen grain type 32. **10**. Pollen grain in SEM, polar view. **11**. Detail of pollen grain surface. **12**. Pollen grain in LM, polar view

# Plates

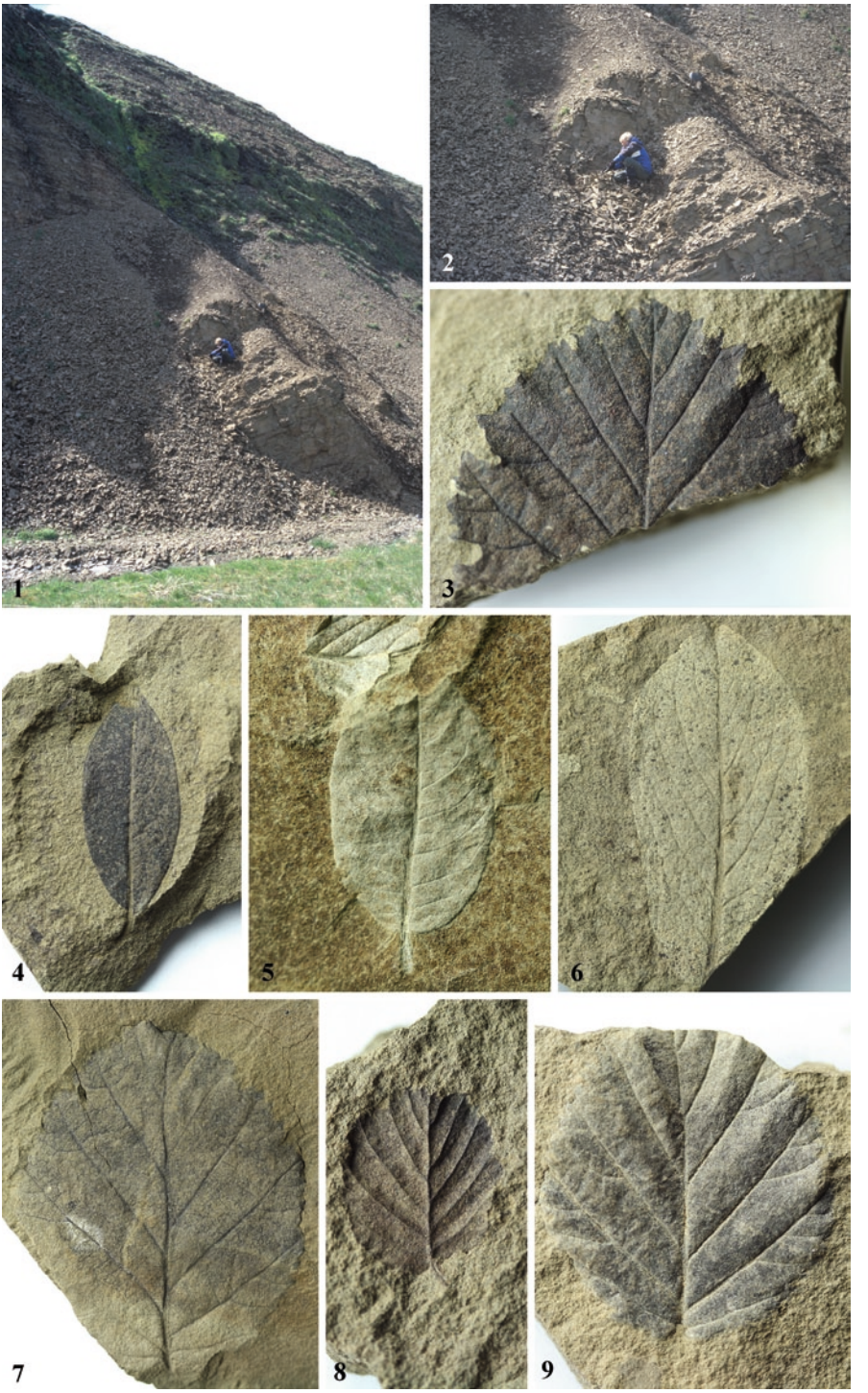



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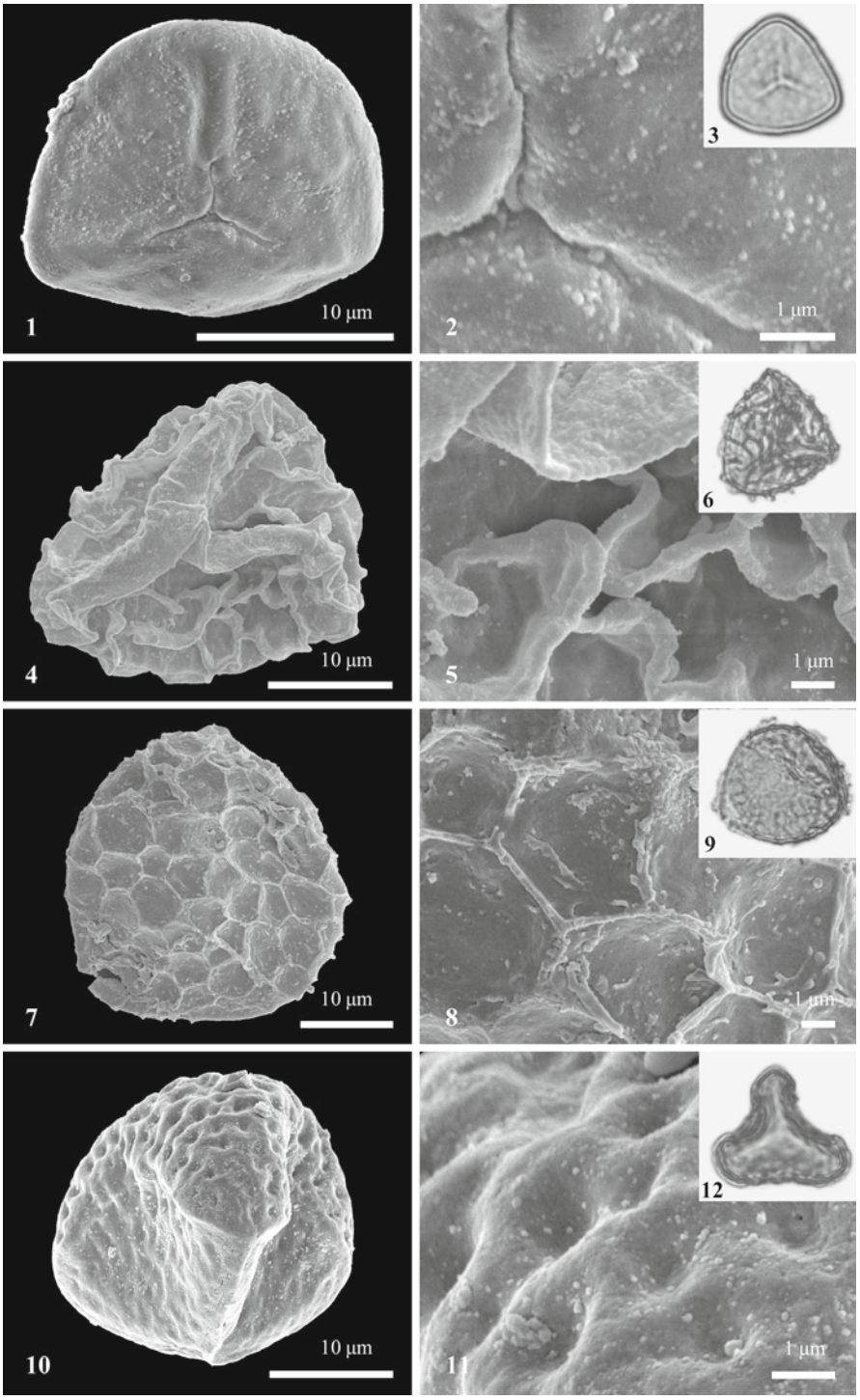



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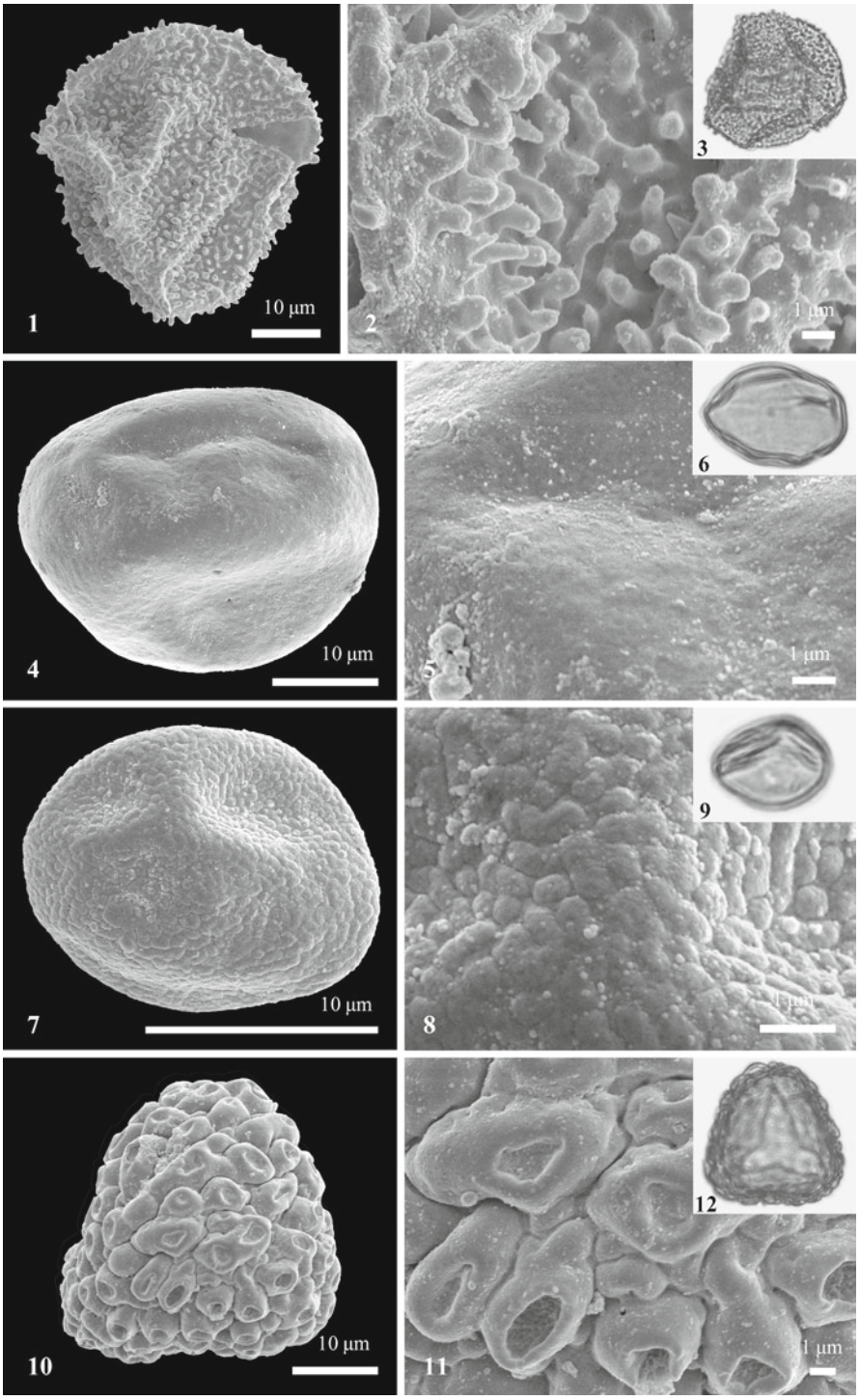



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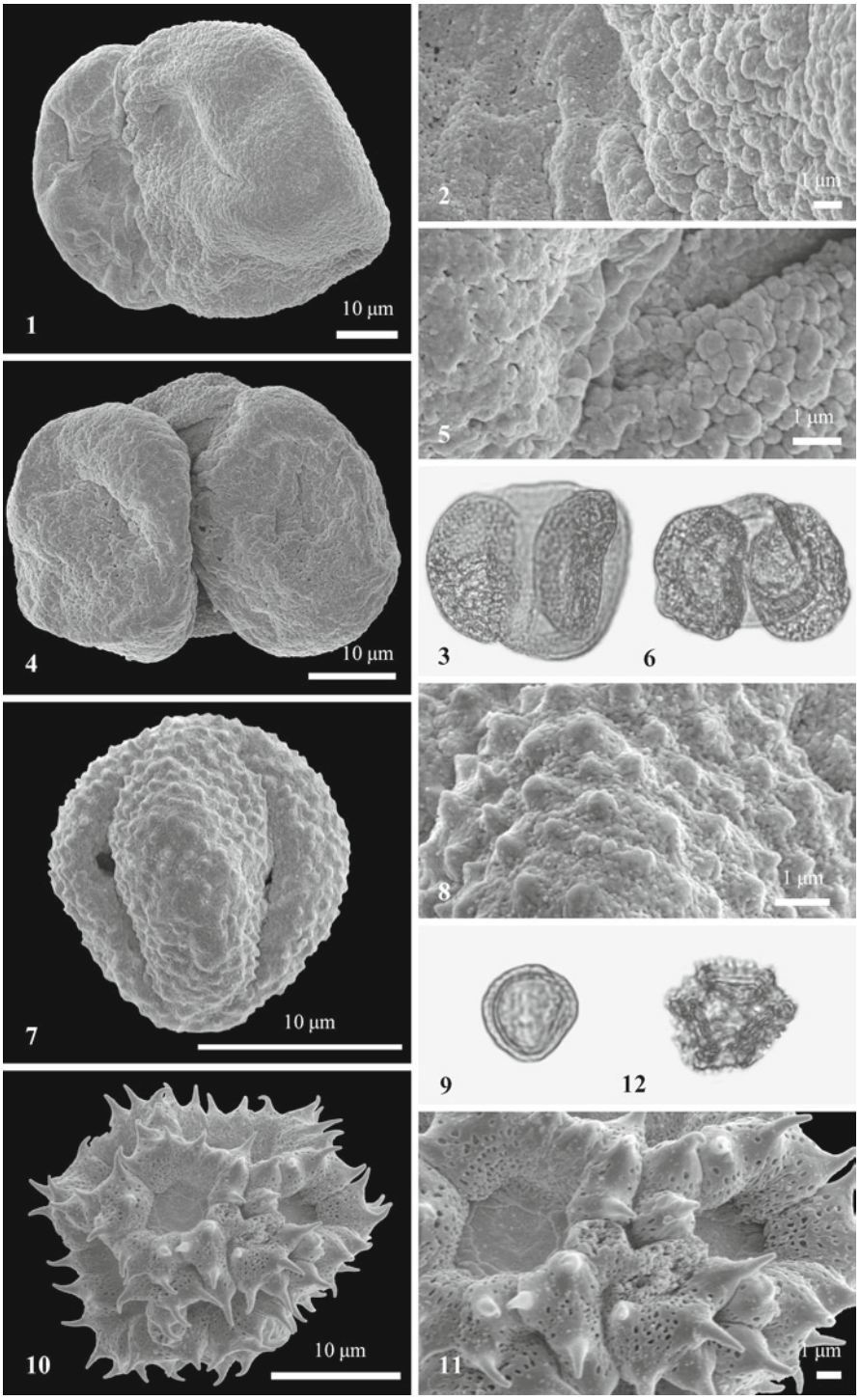



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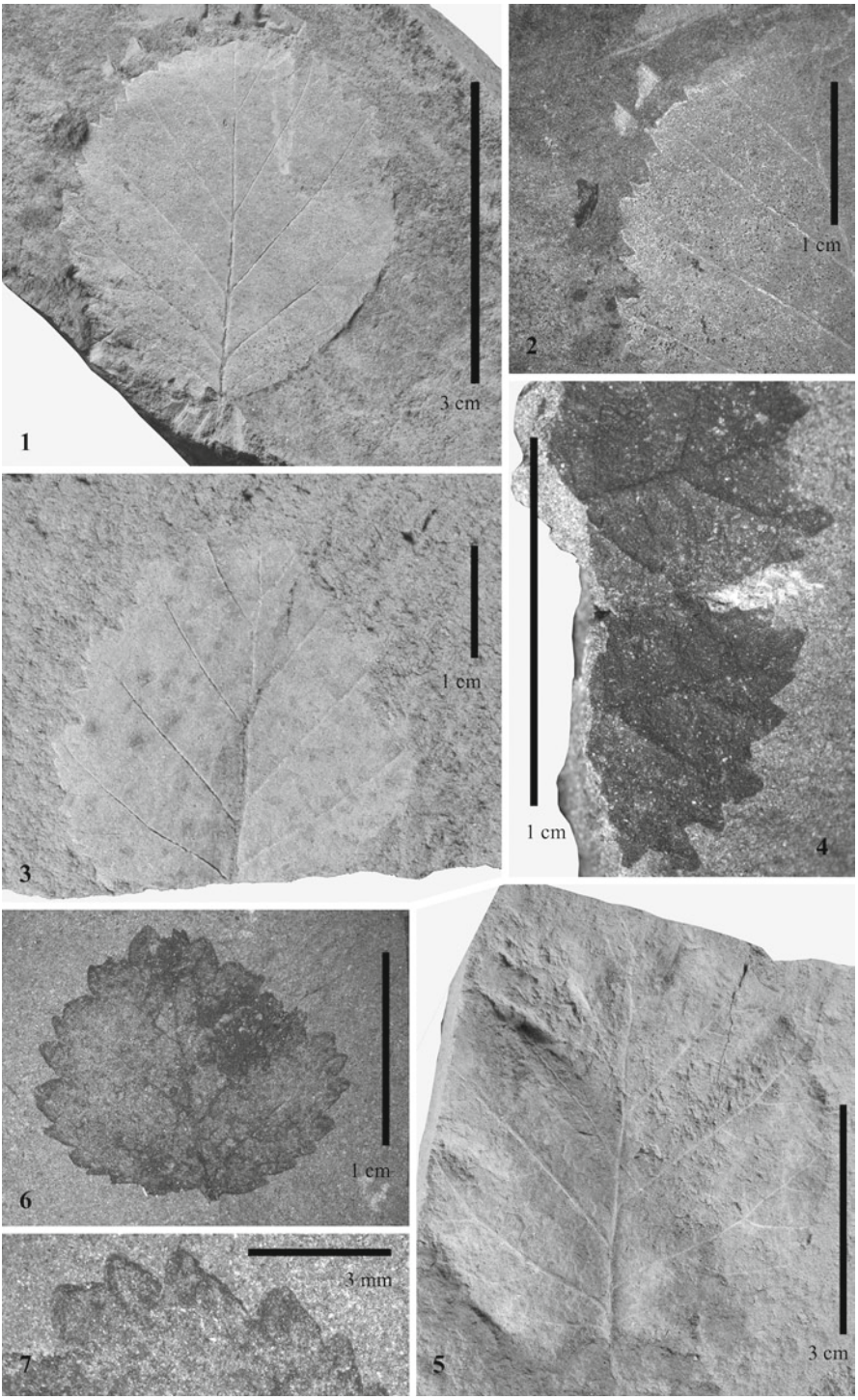



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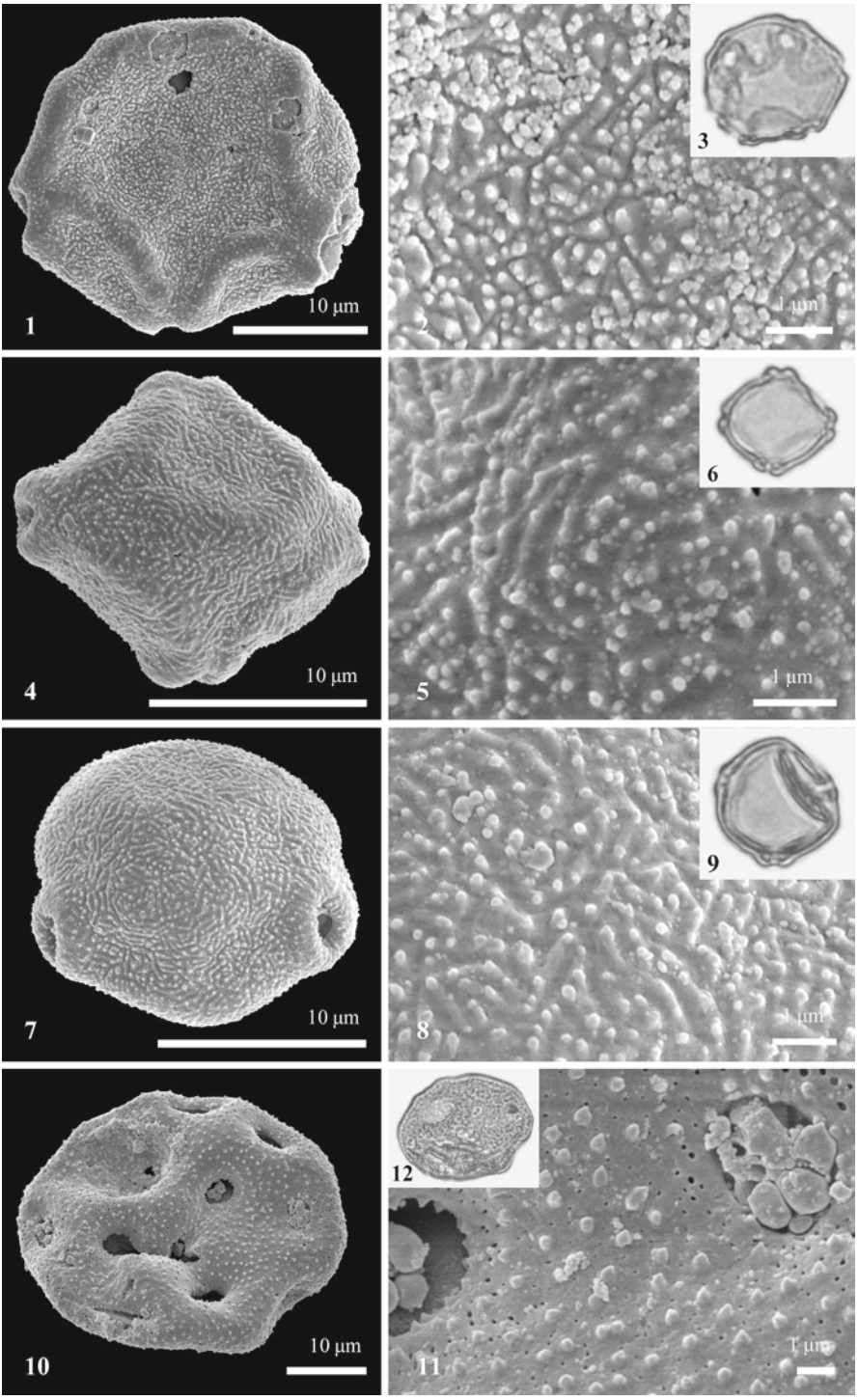



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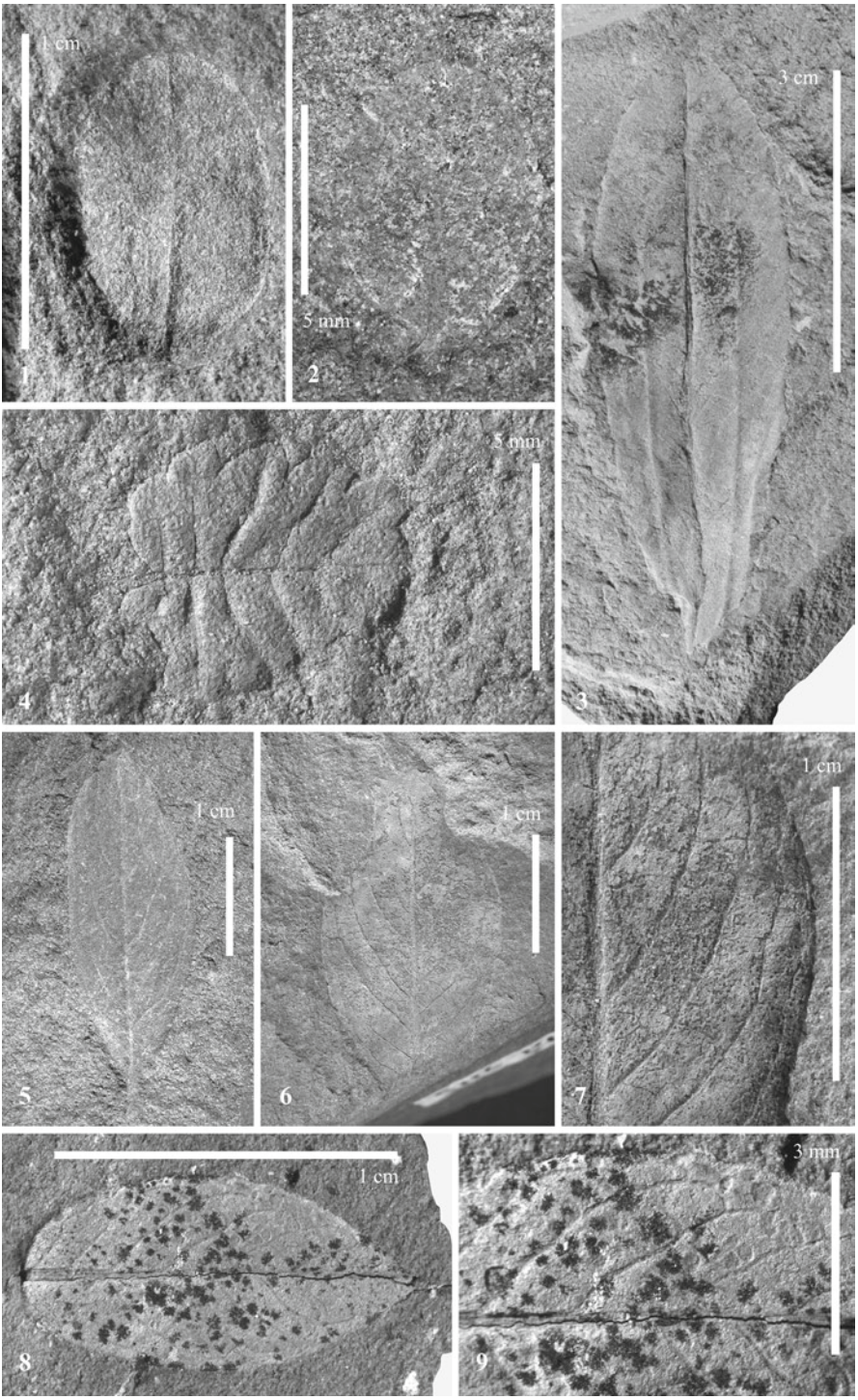



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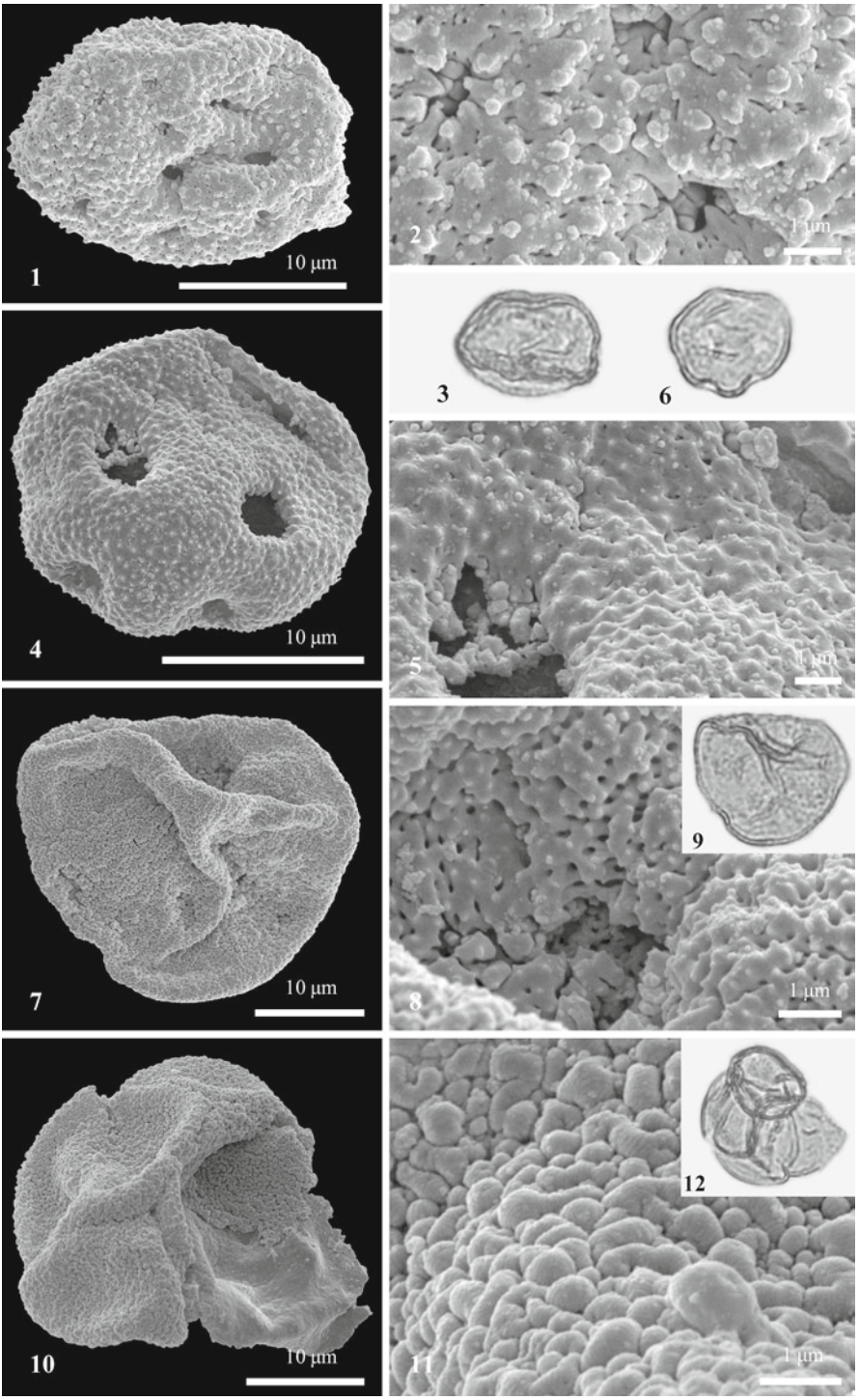



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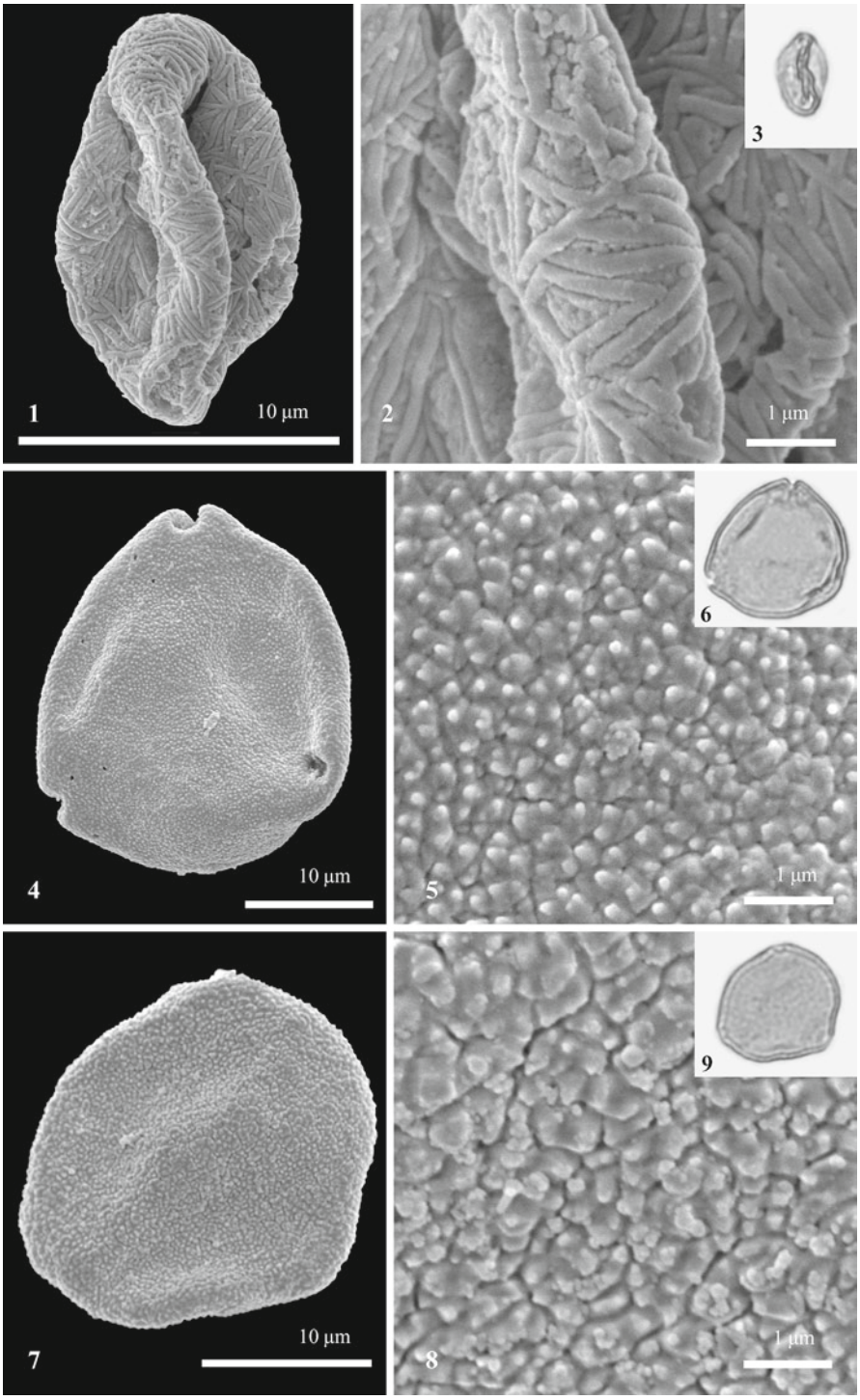



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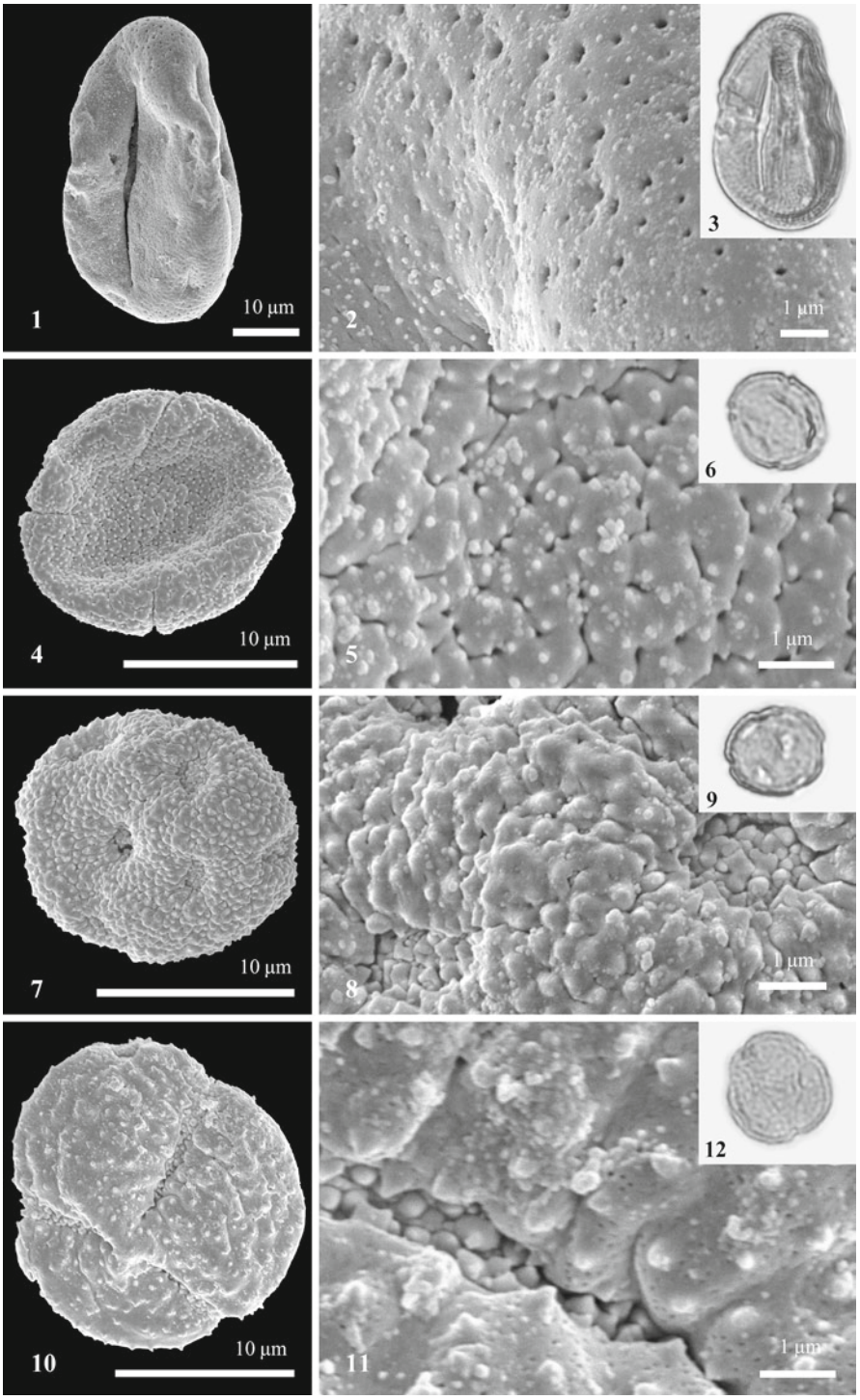



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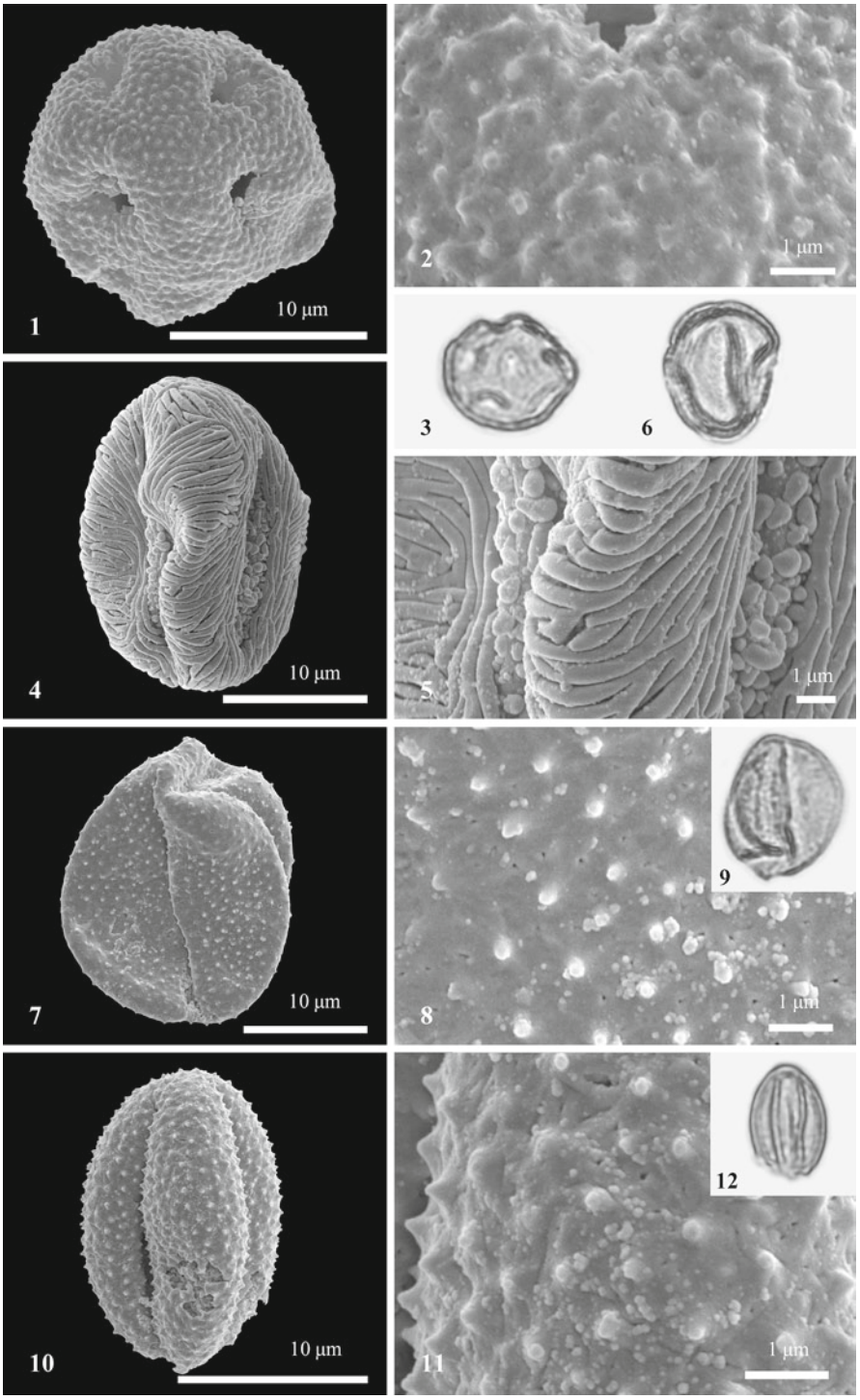



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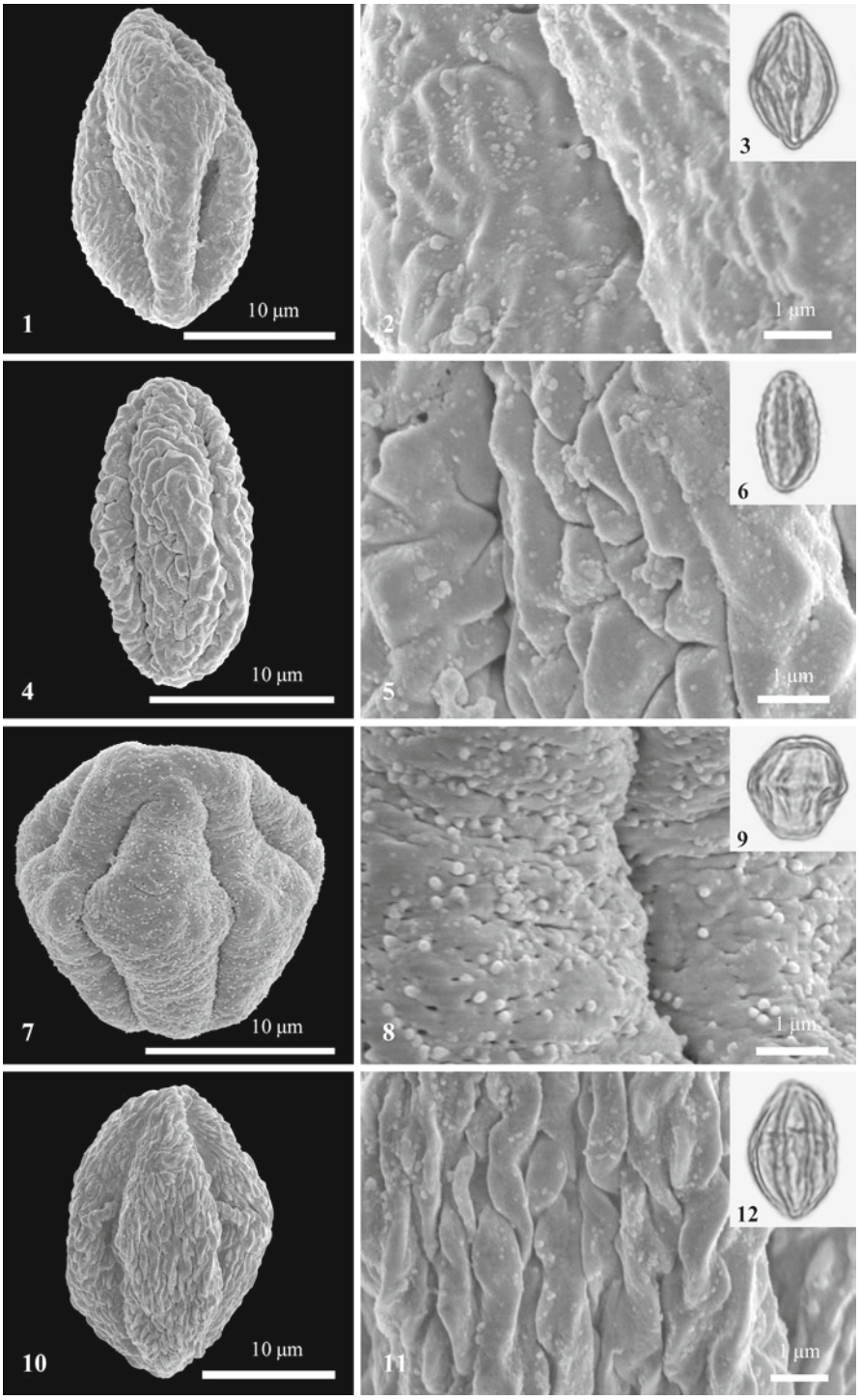



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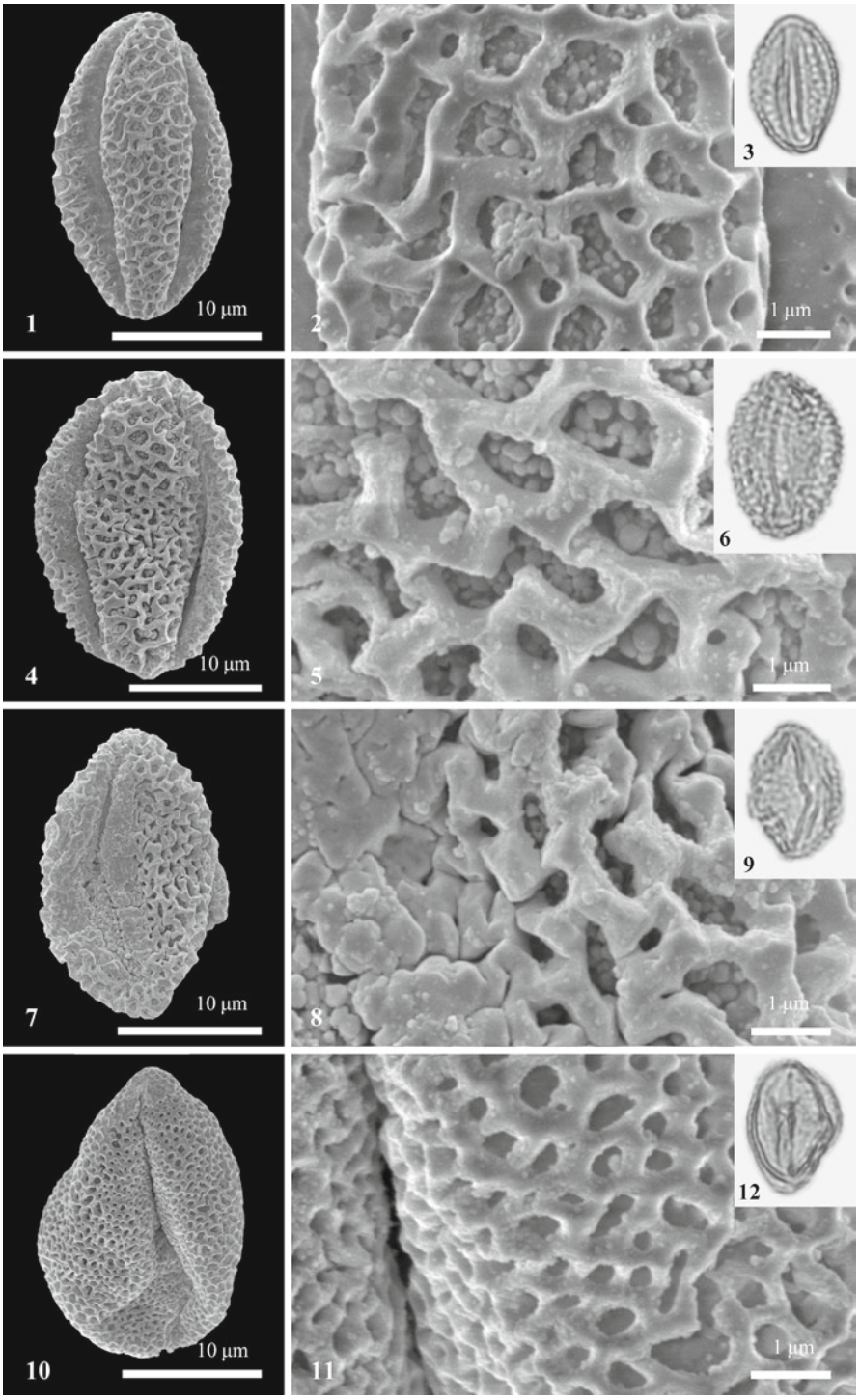



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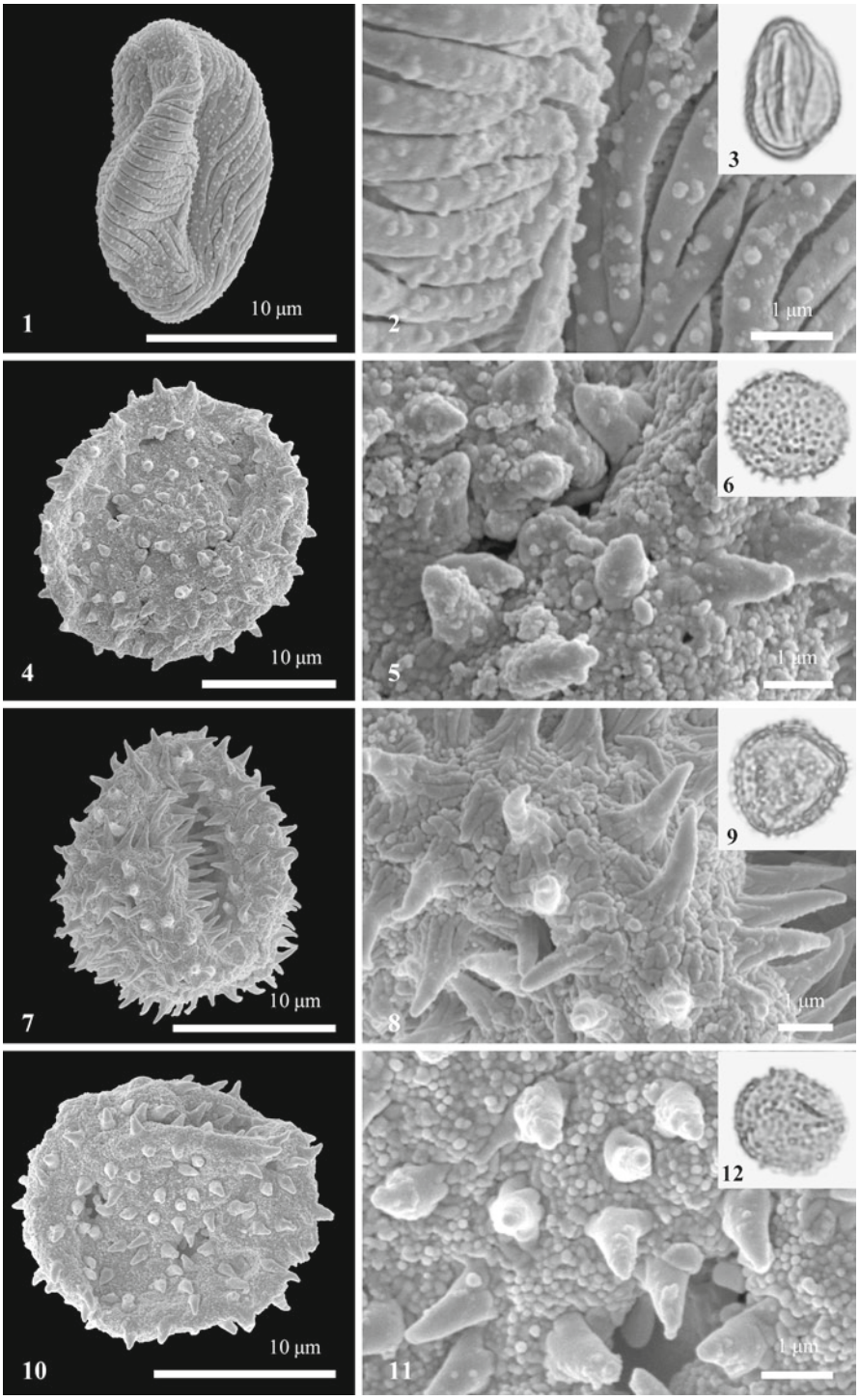



**Plate 11.14**




**Plate 11.15**

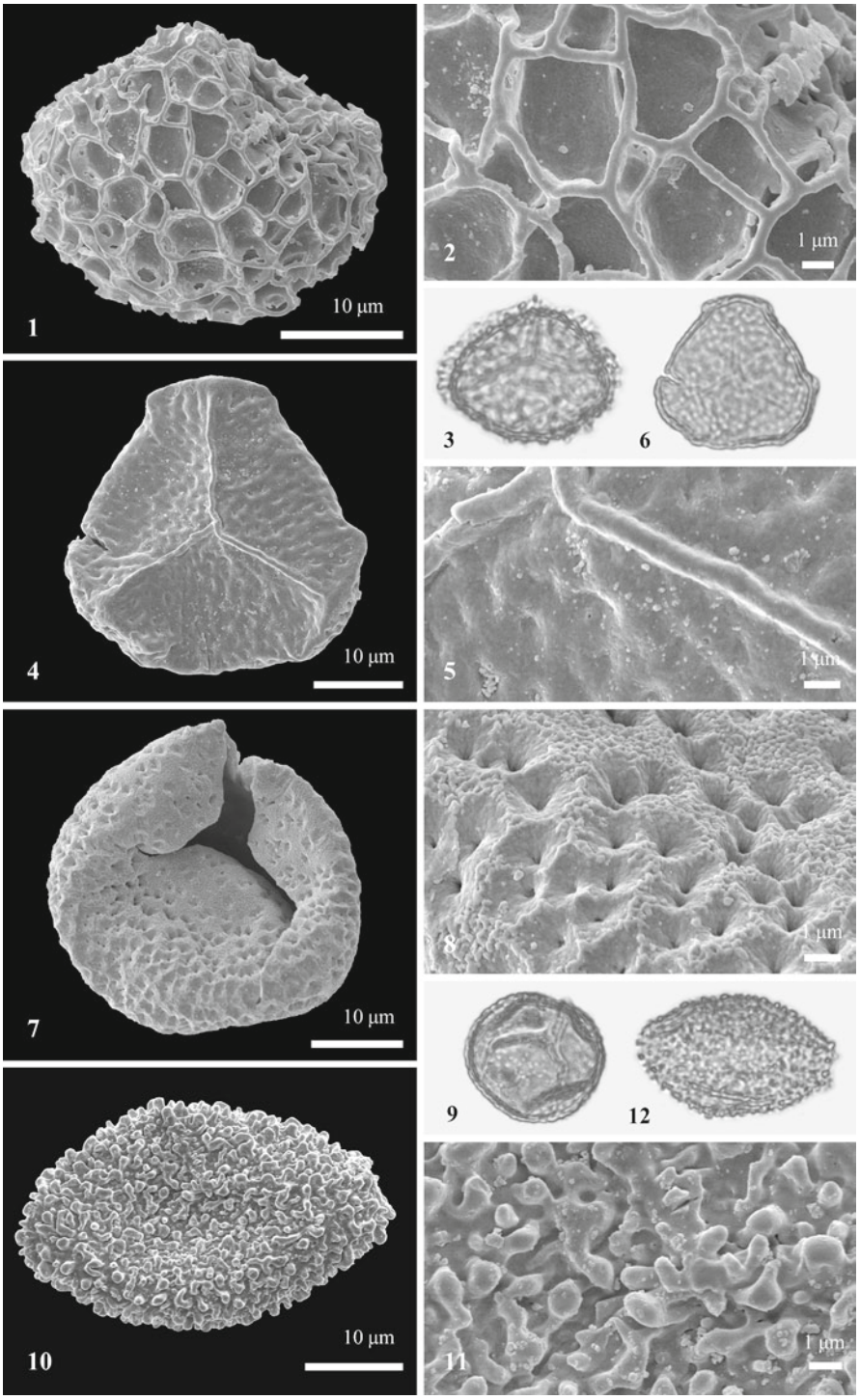



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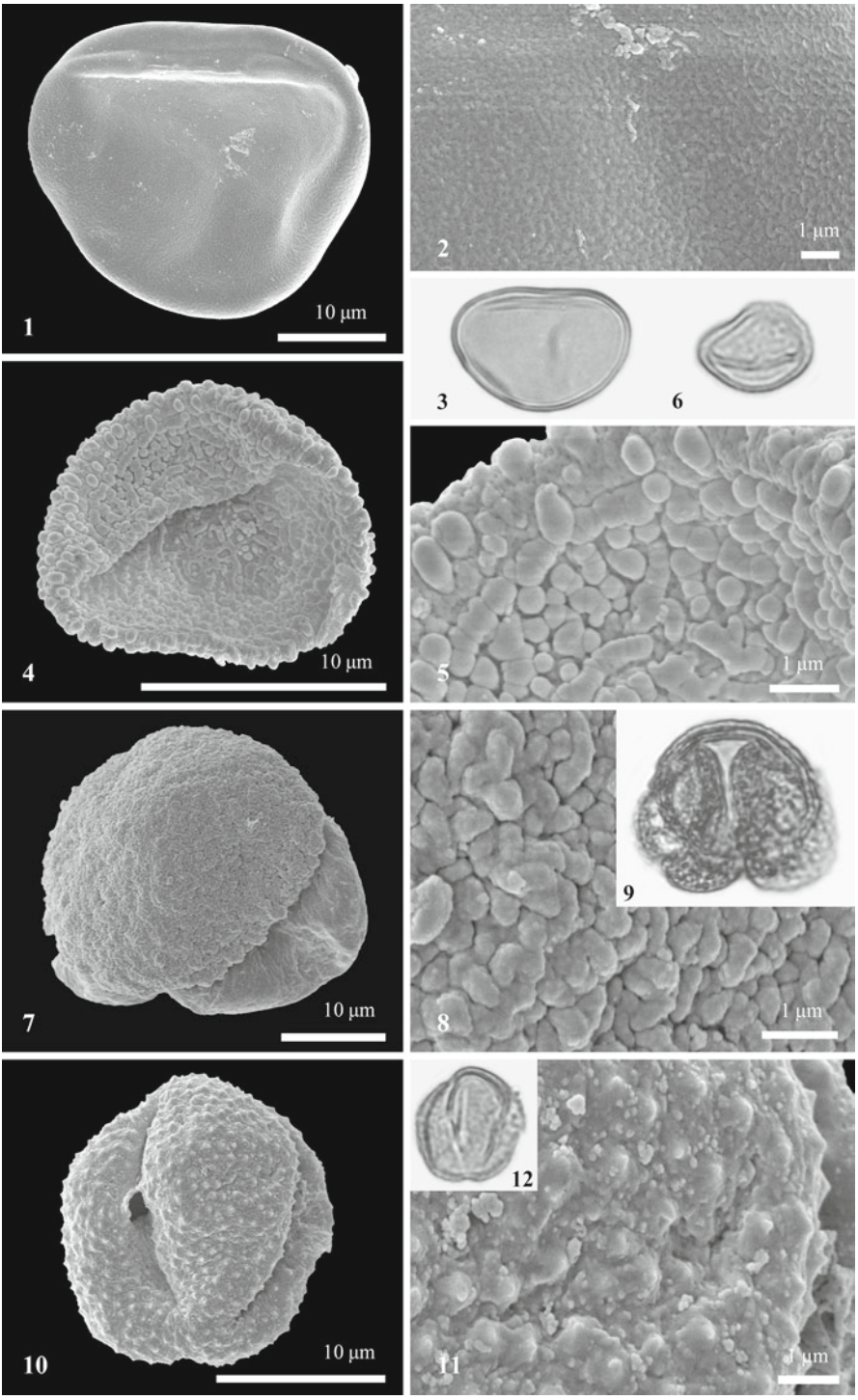



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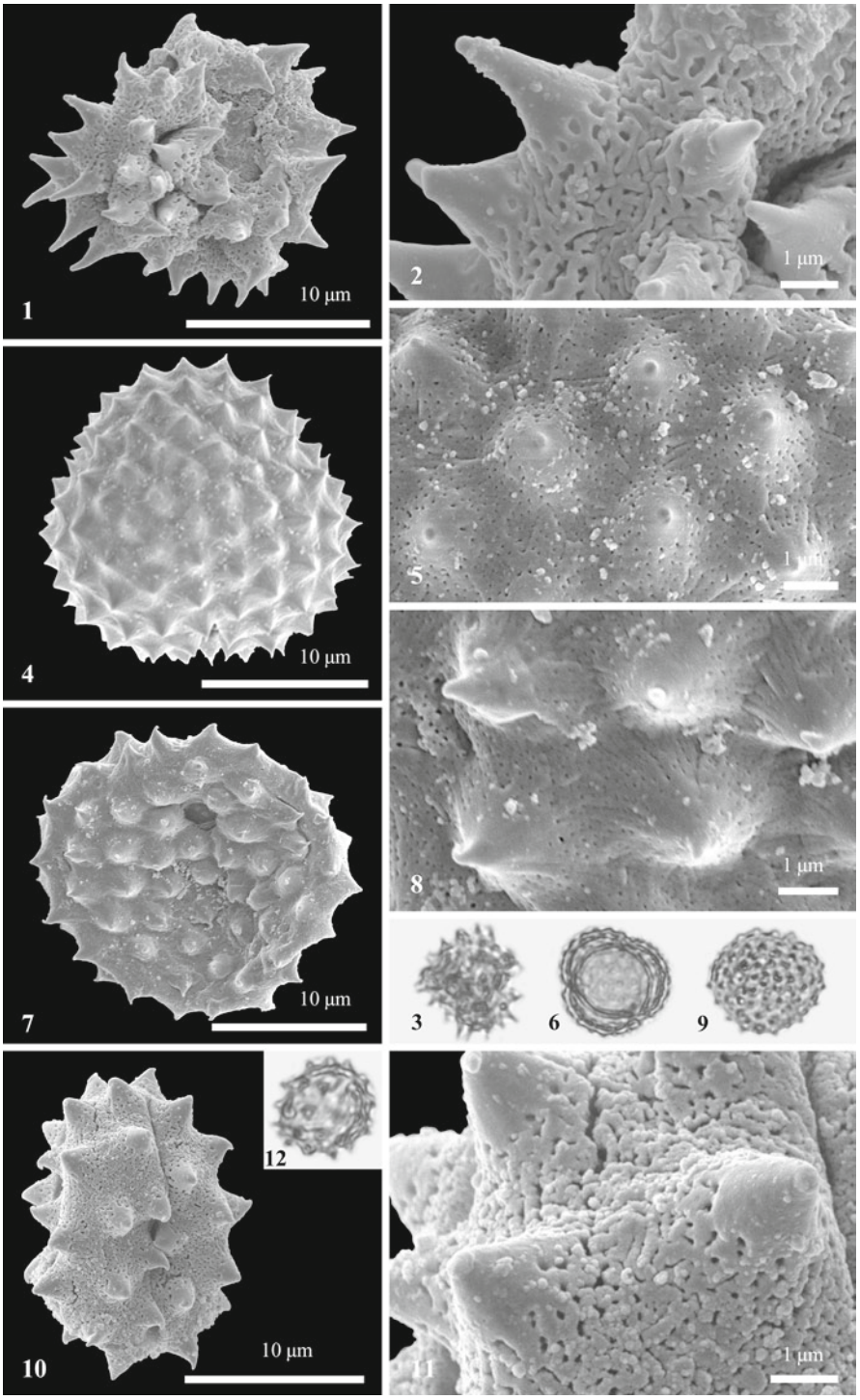



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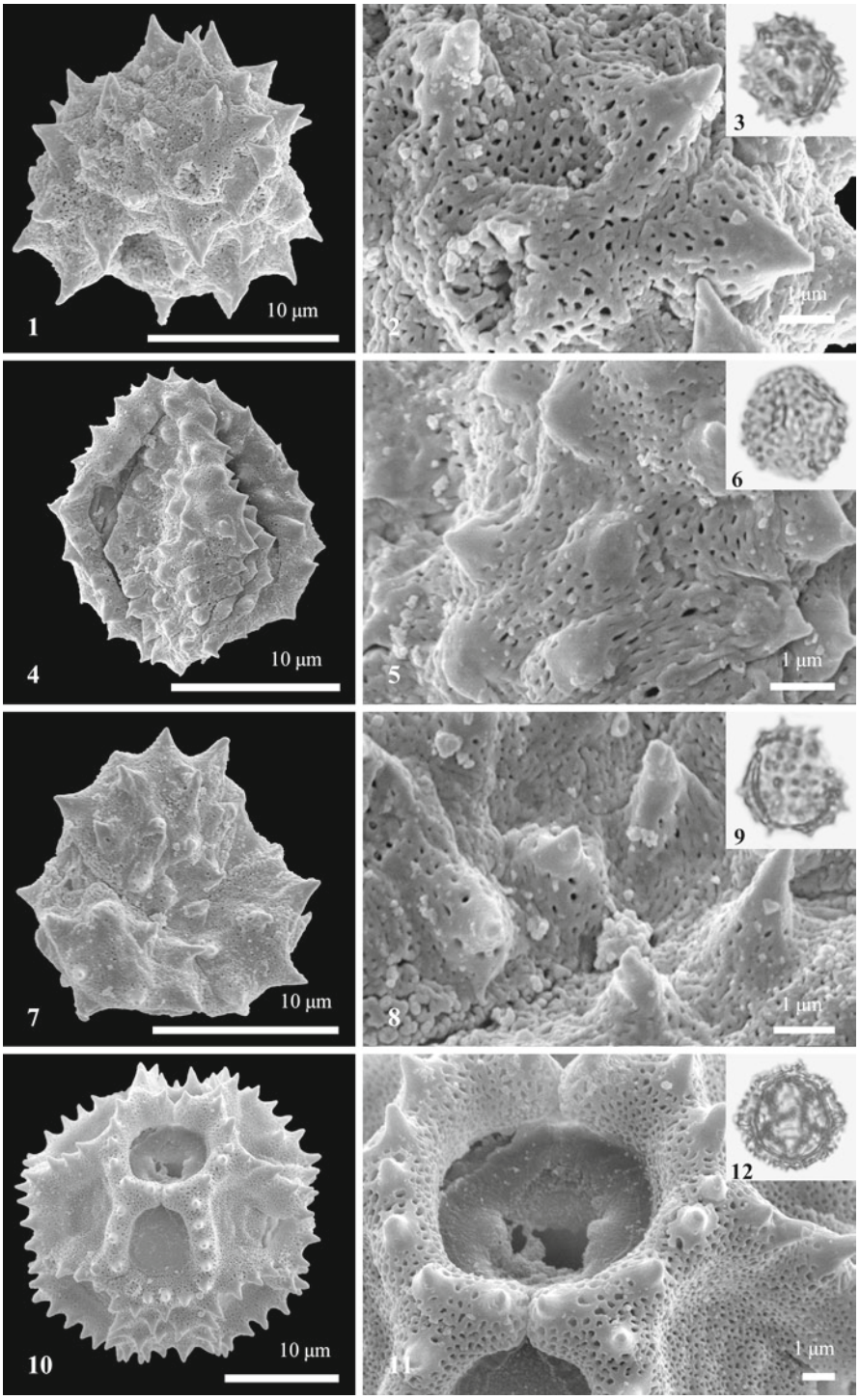



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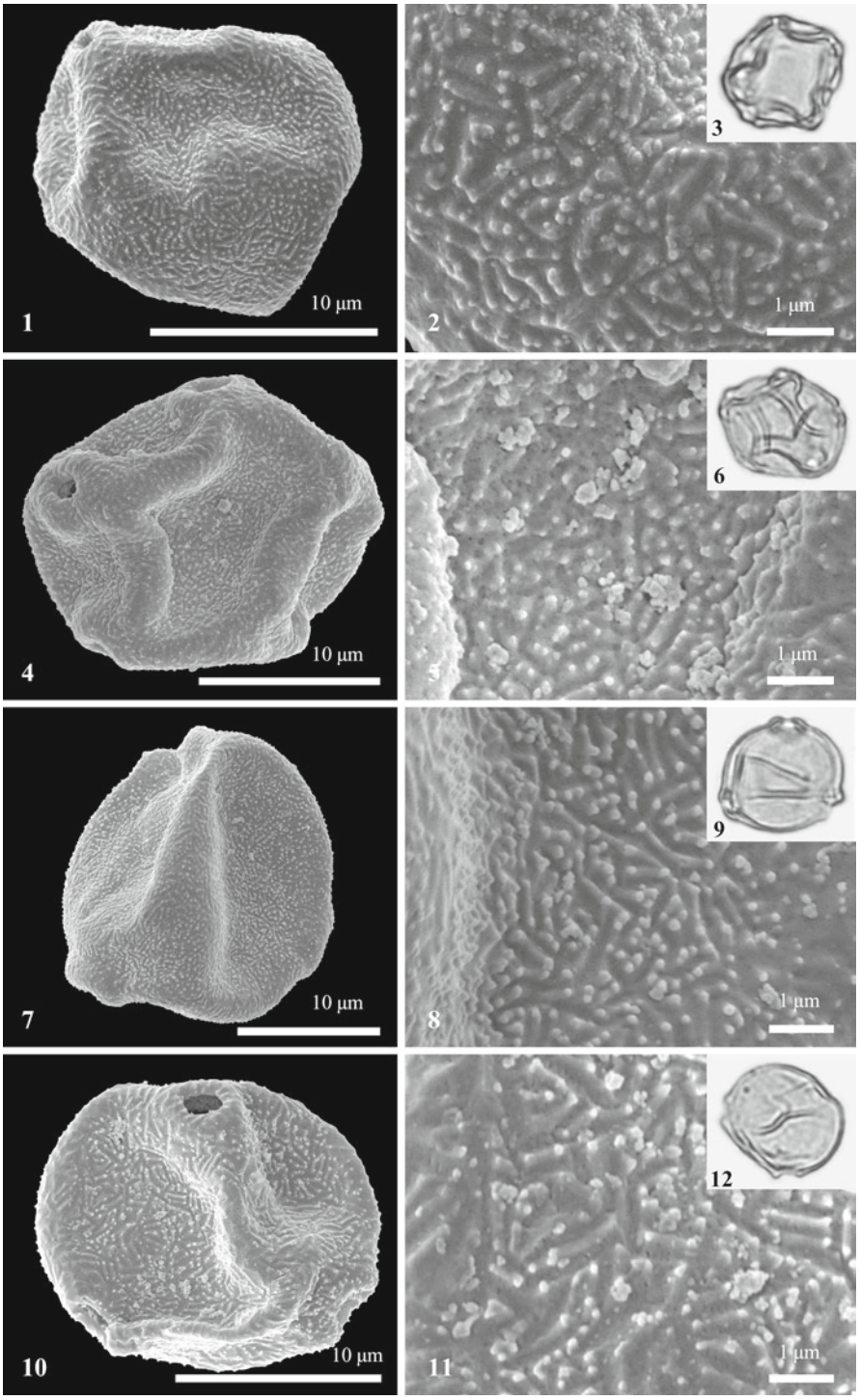



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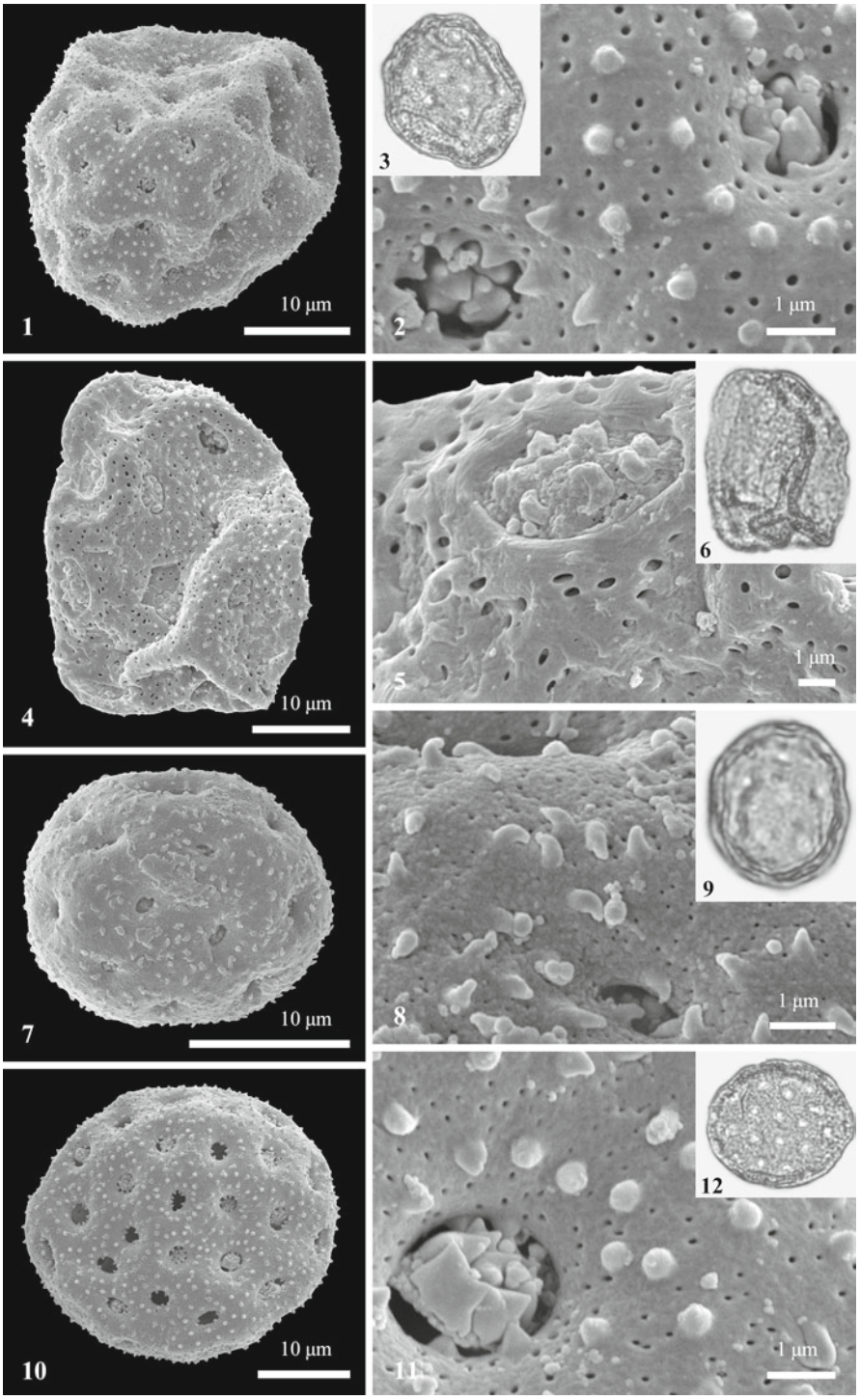



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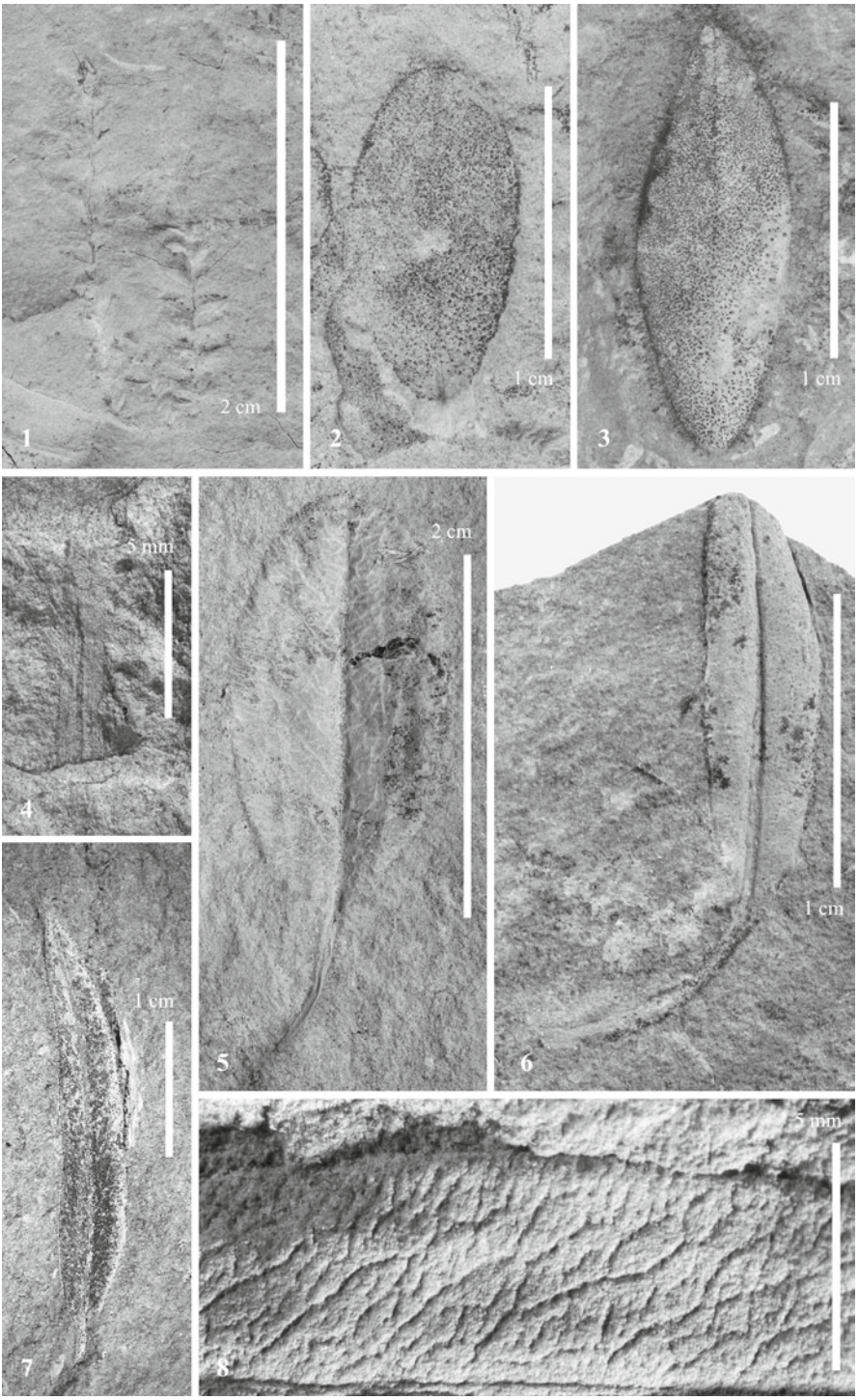



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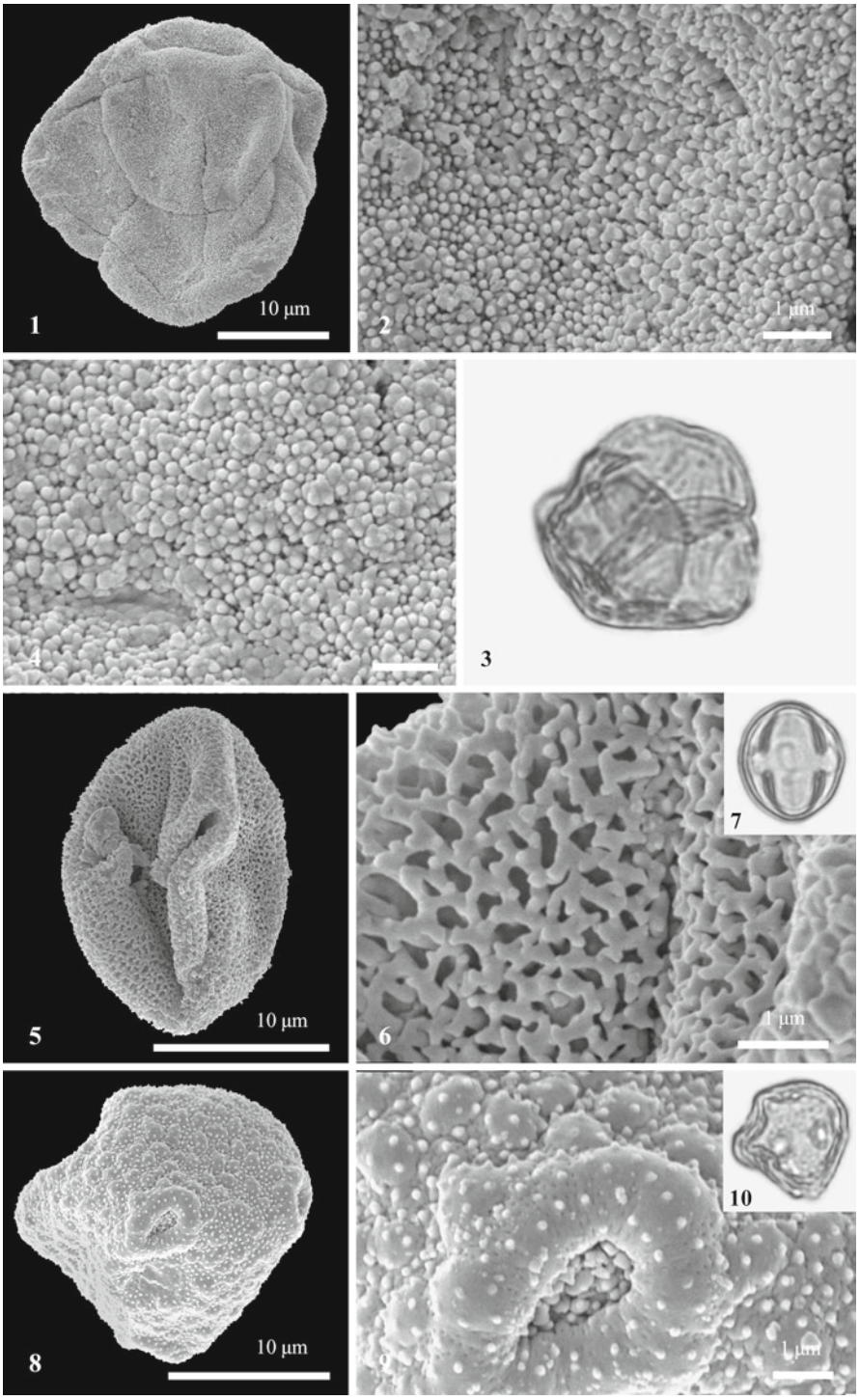



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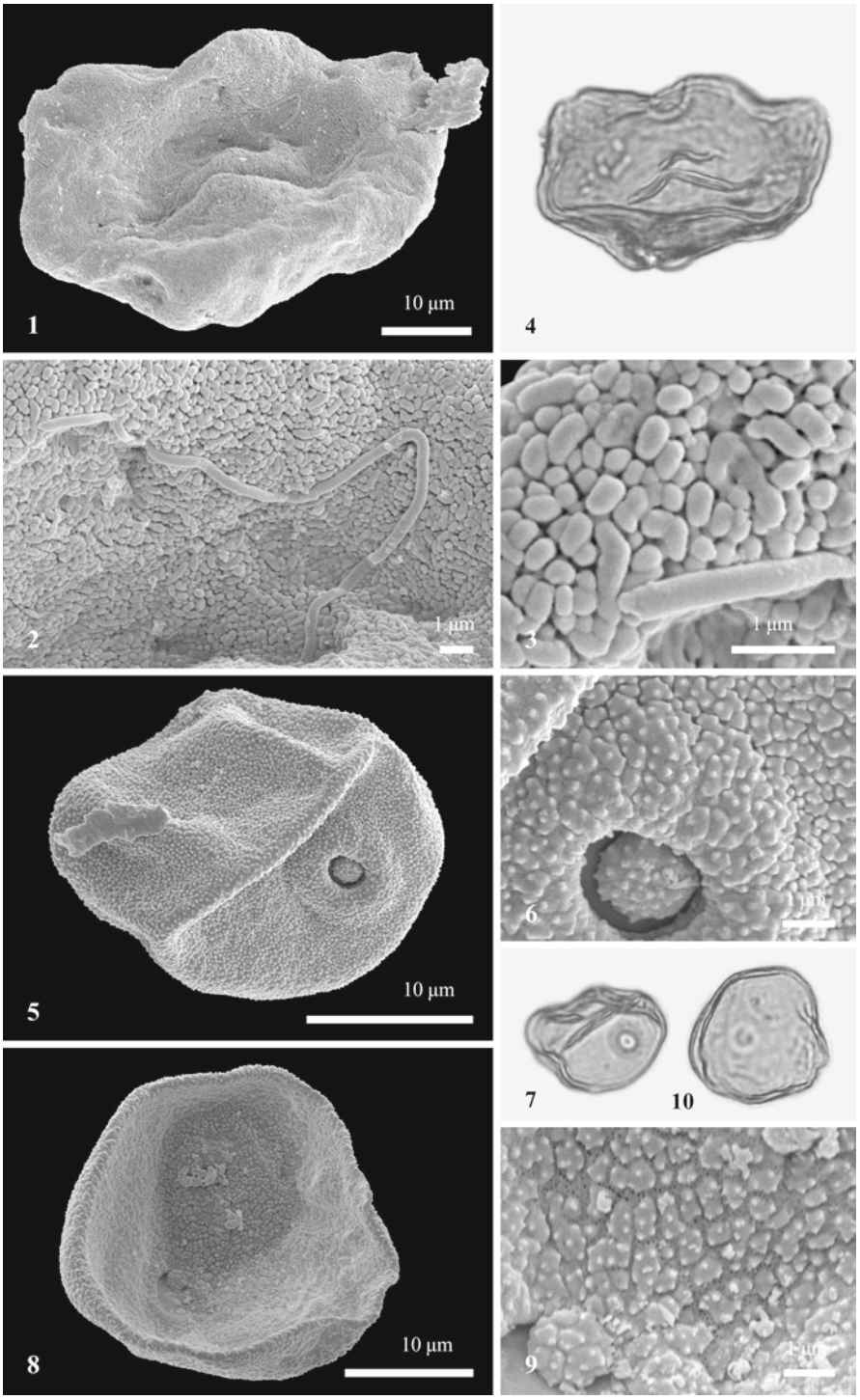



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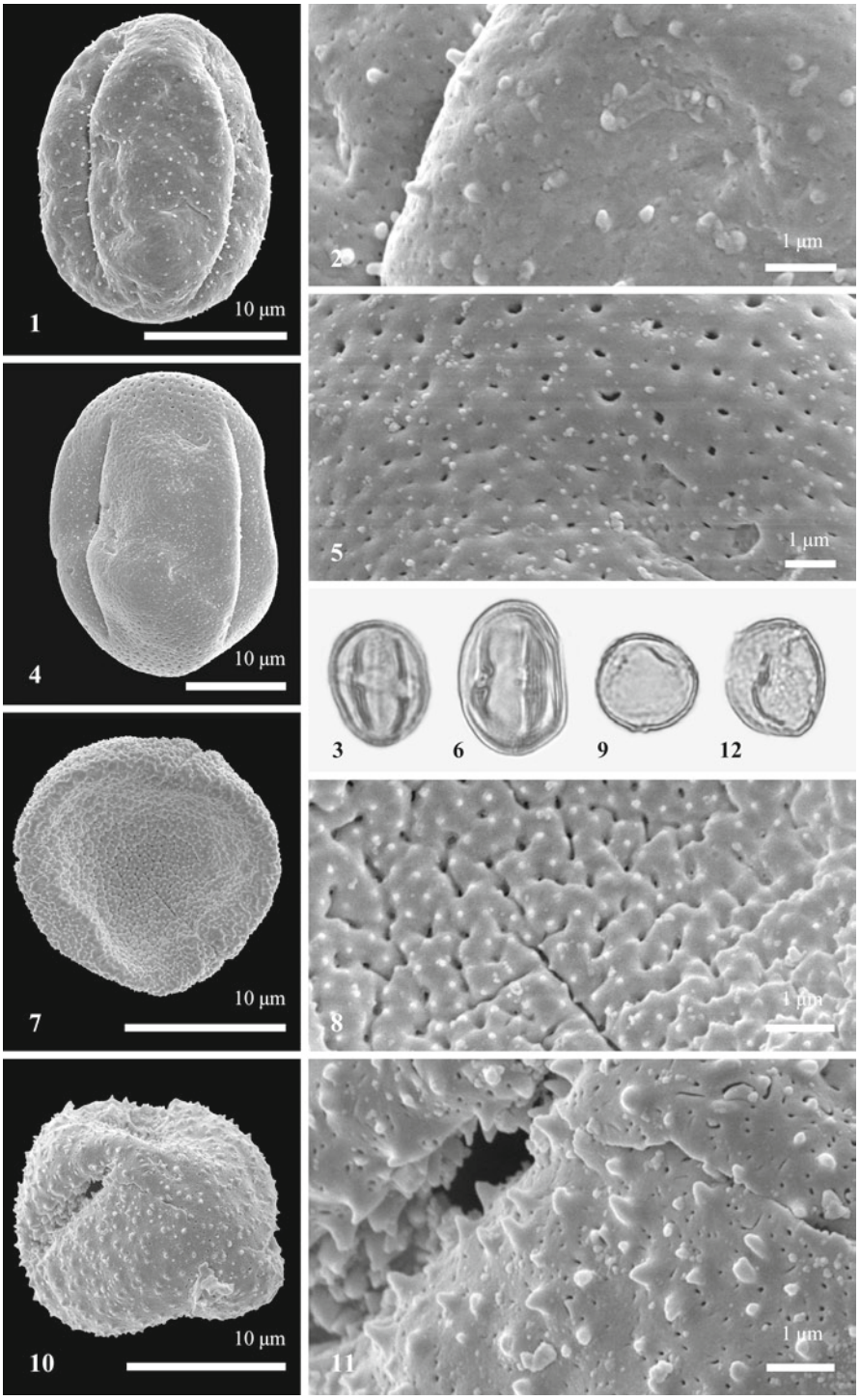



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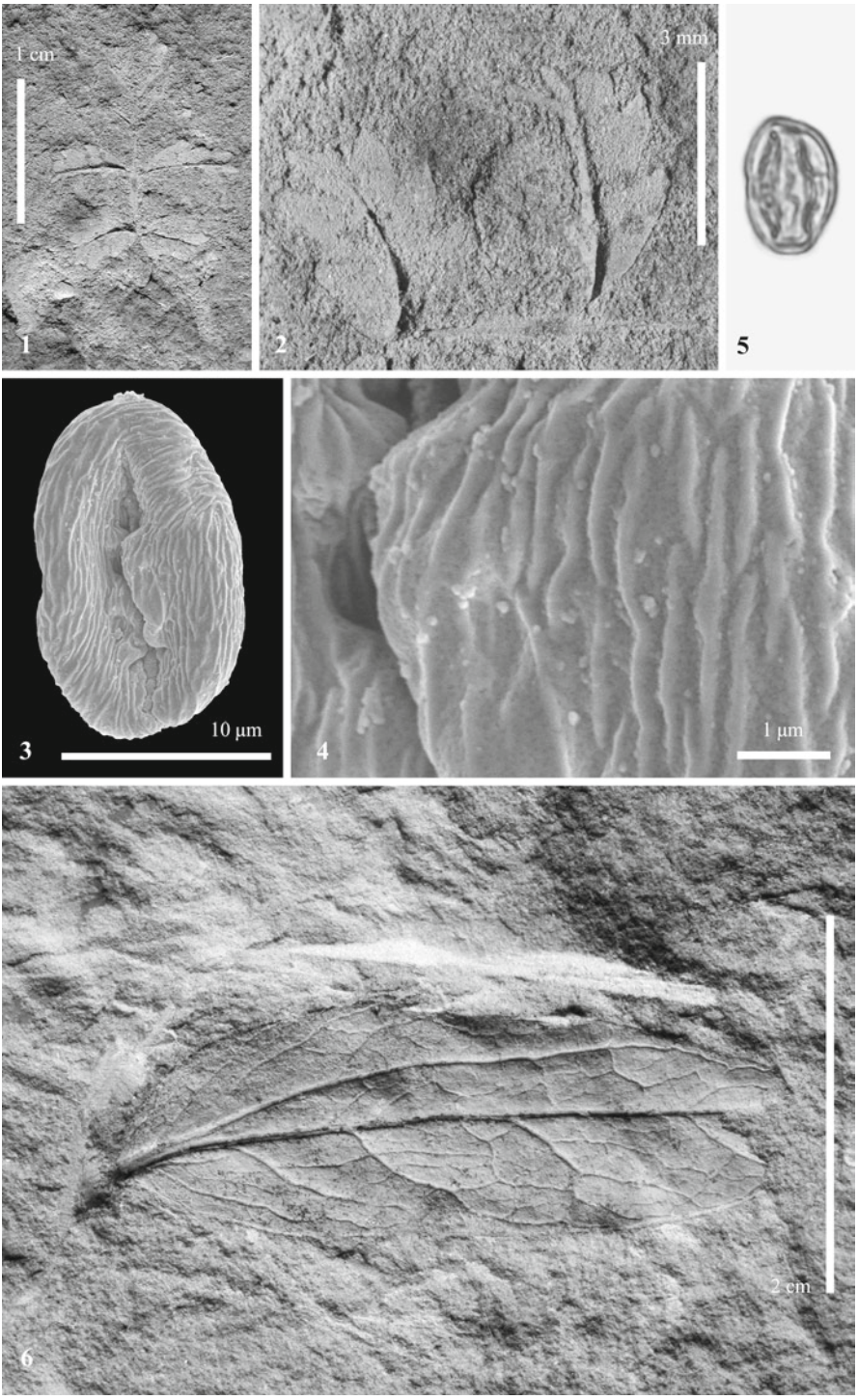



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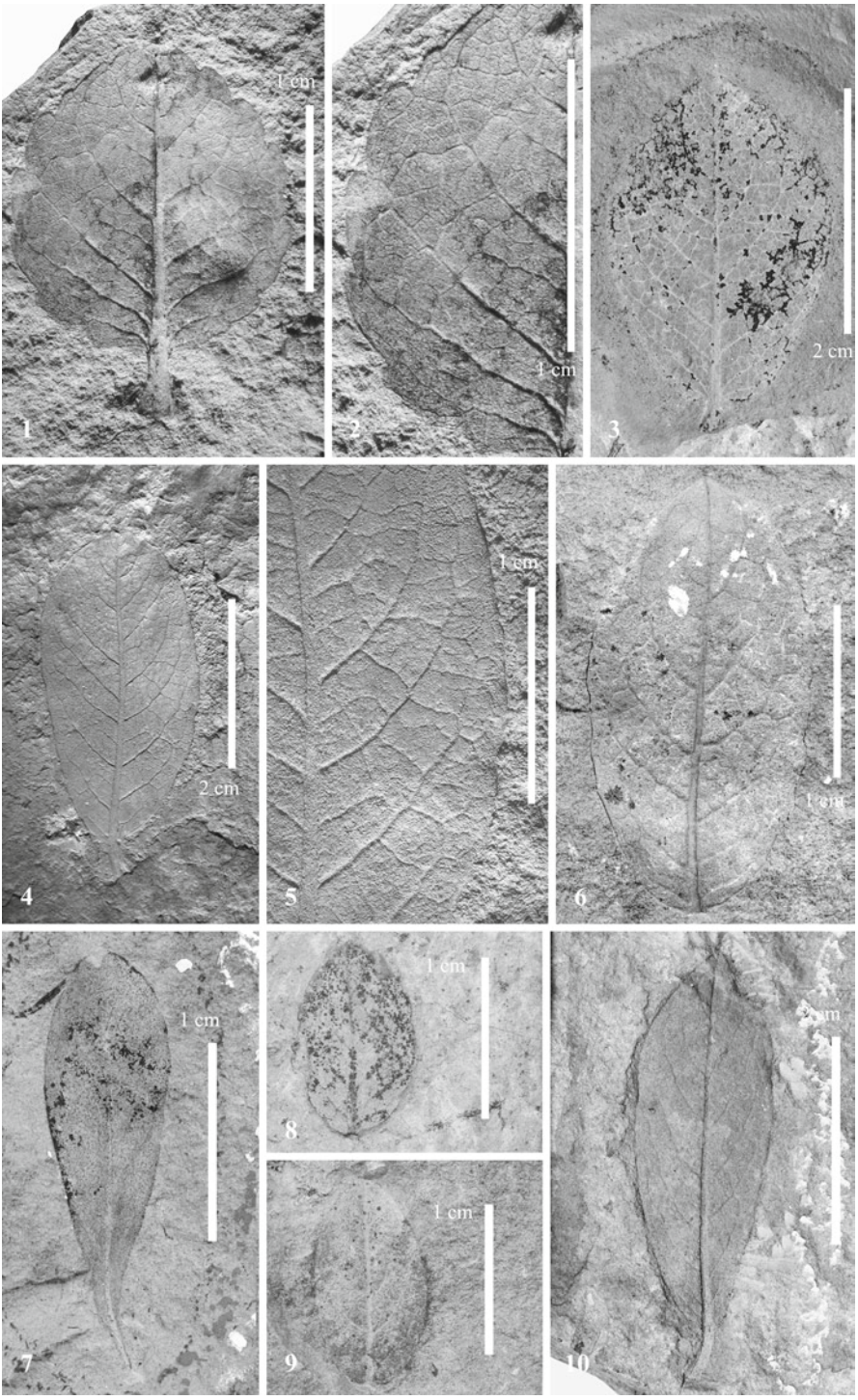



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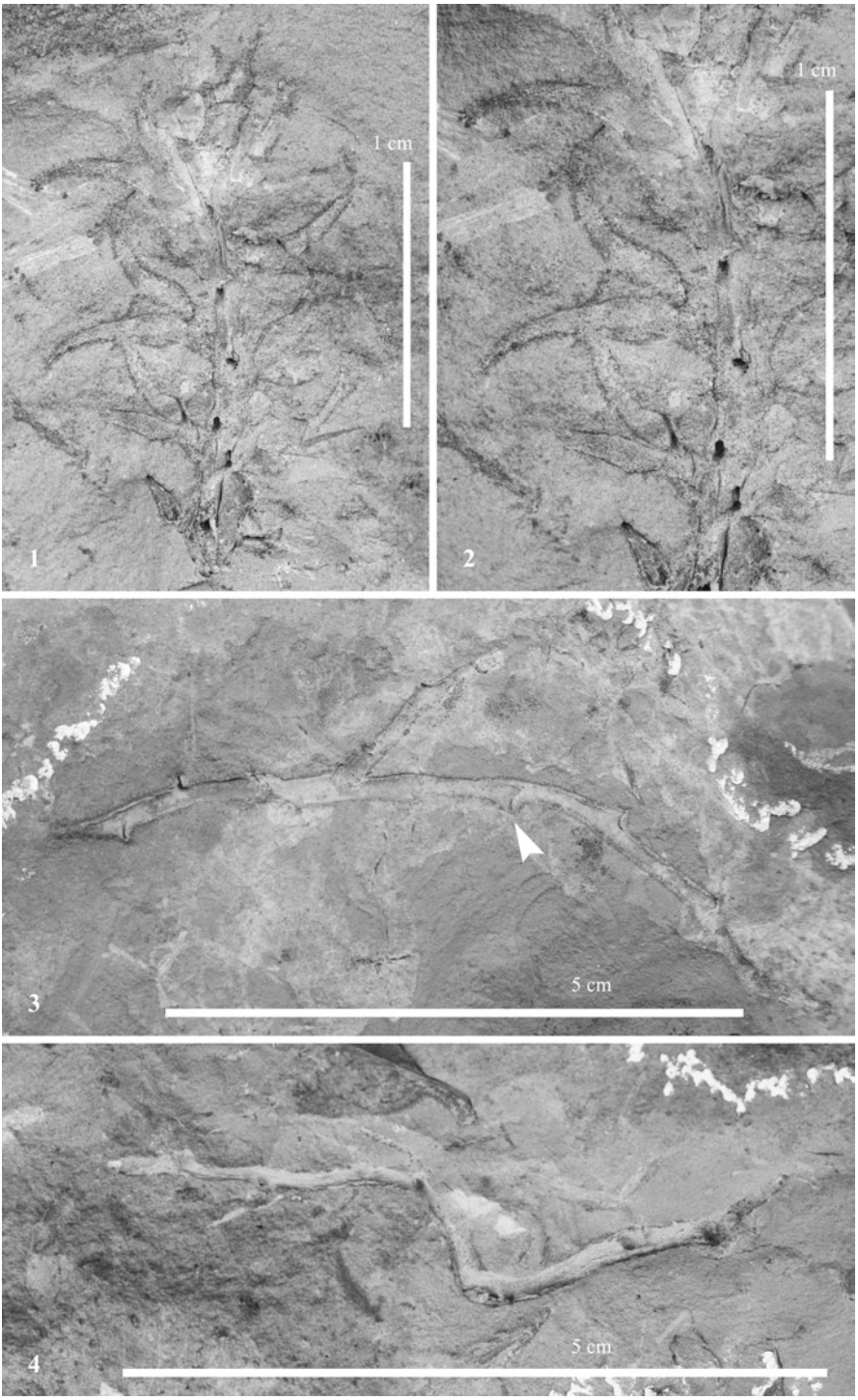



**Plate 11.28**

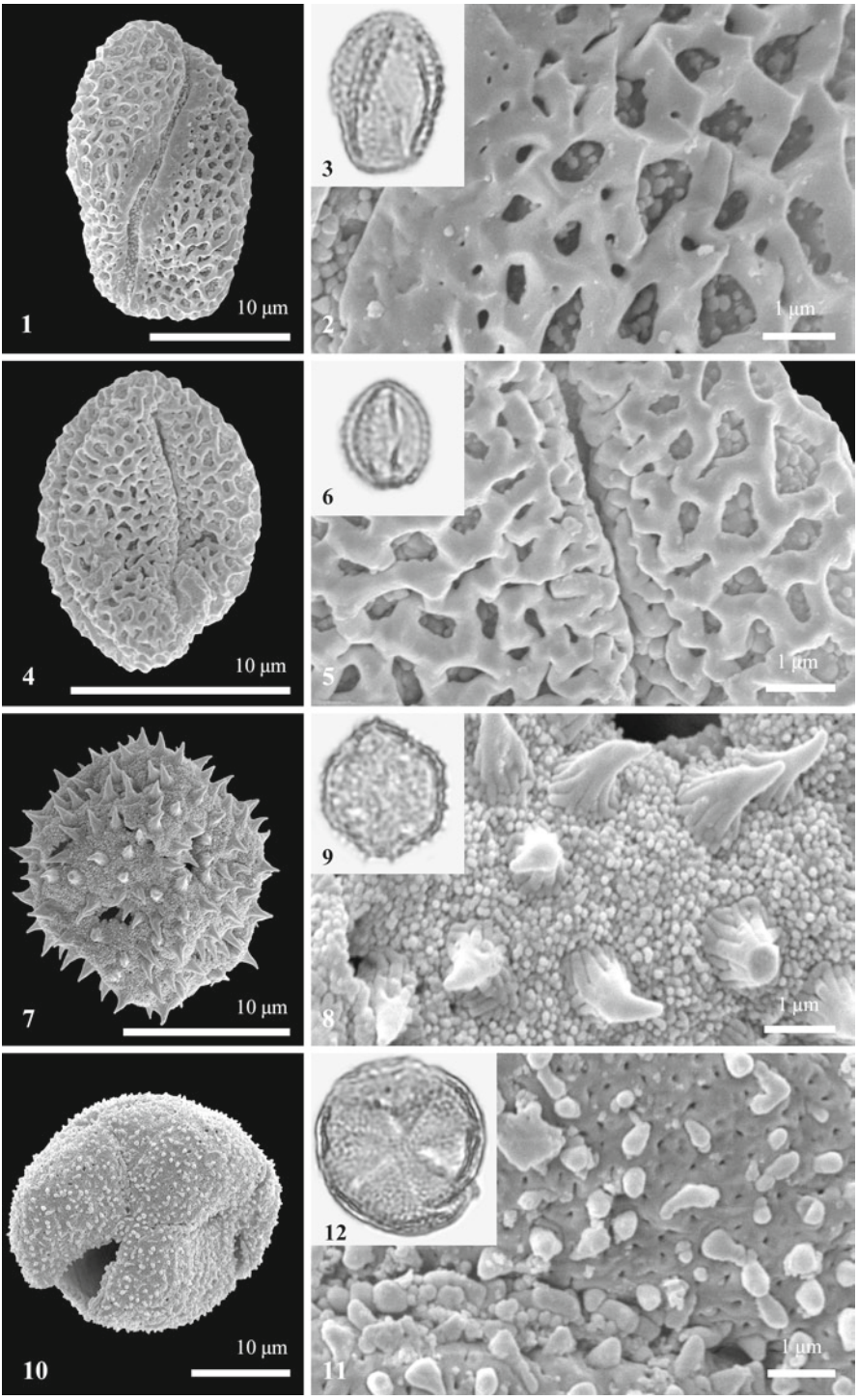



**Plate 11.29**




**Plate 11.30**

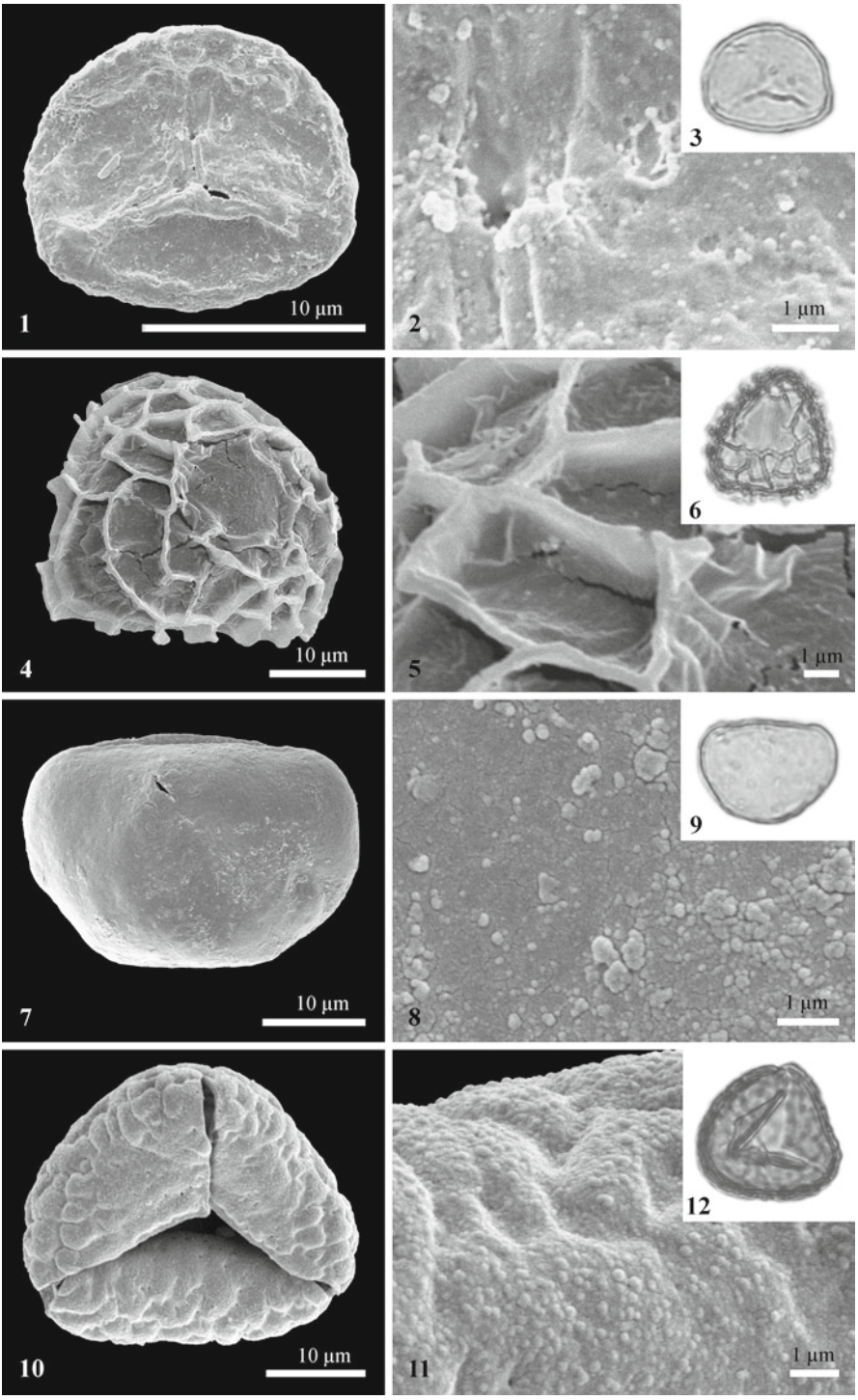



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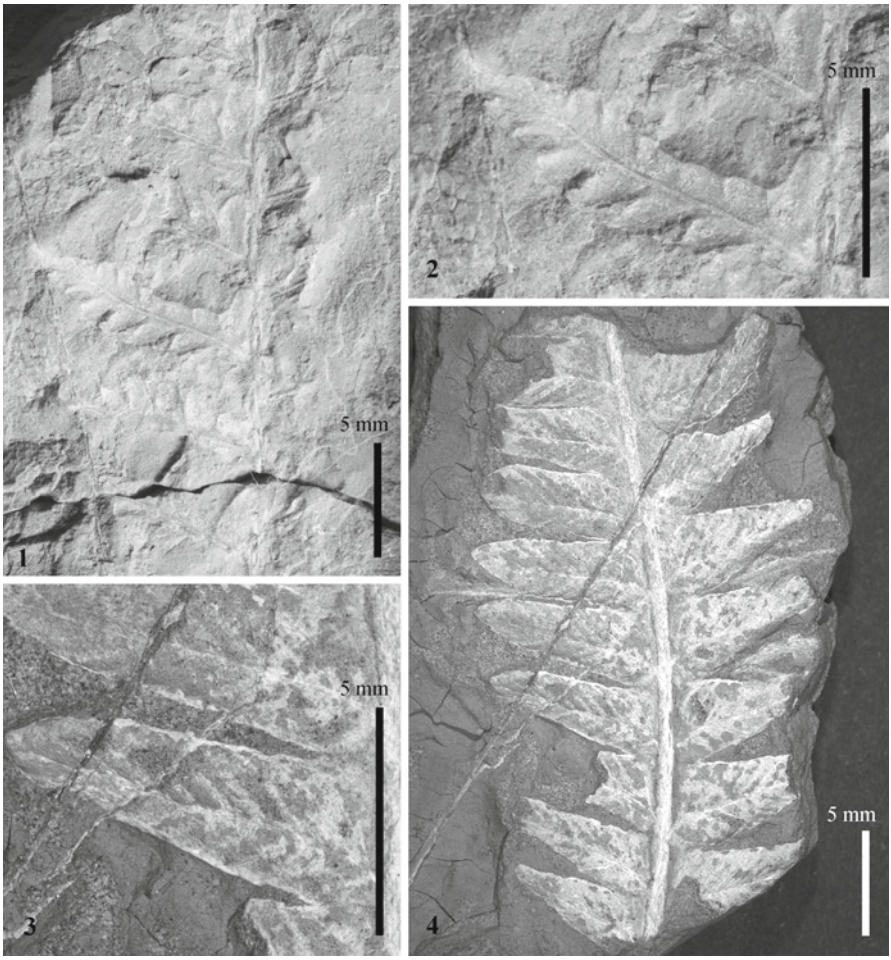



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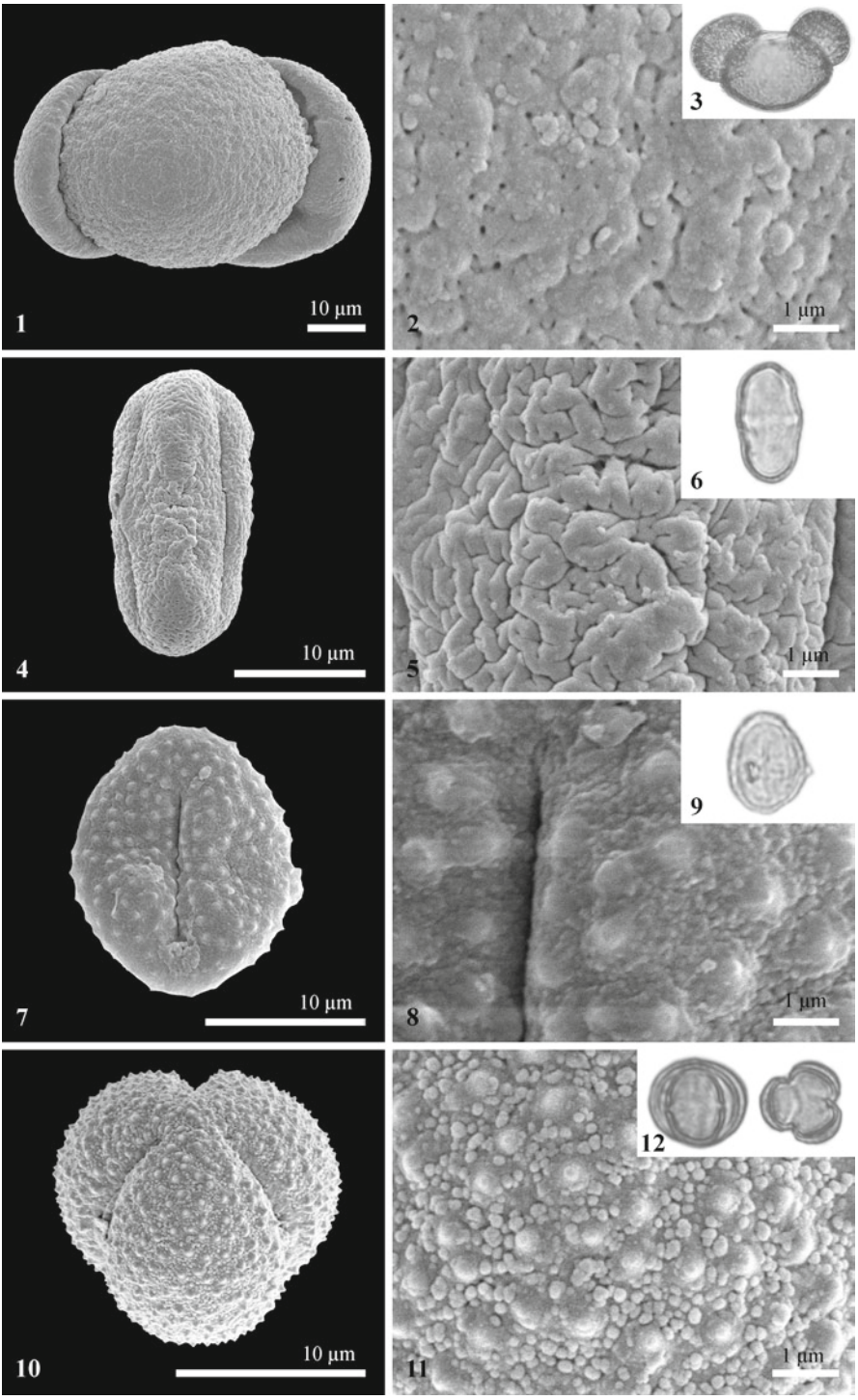



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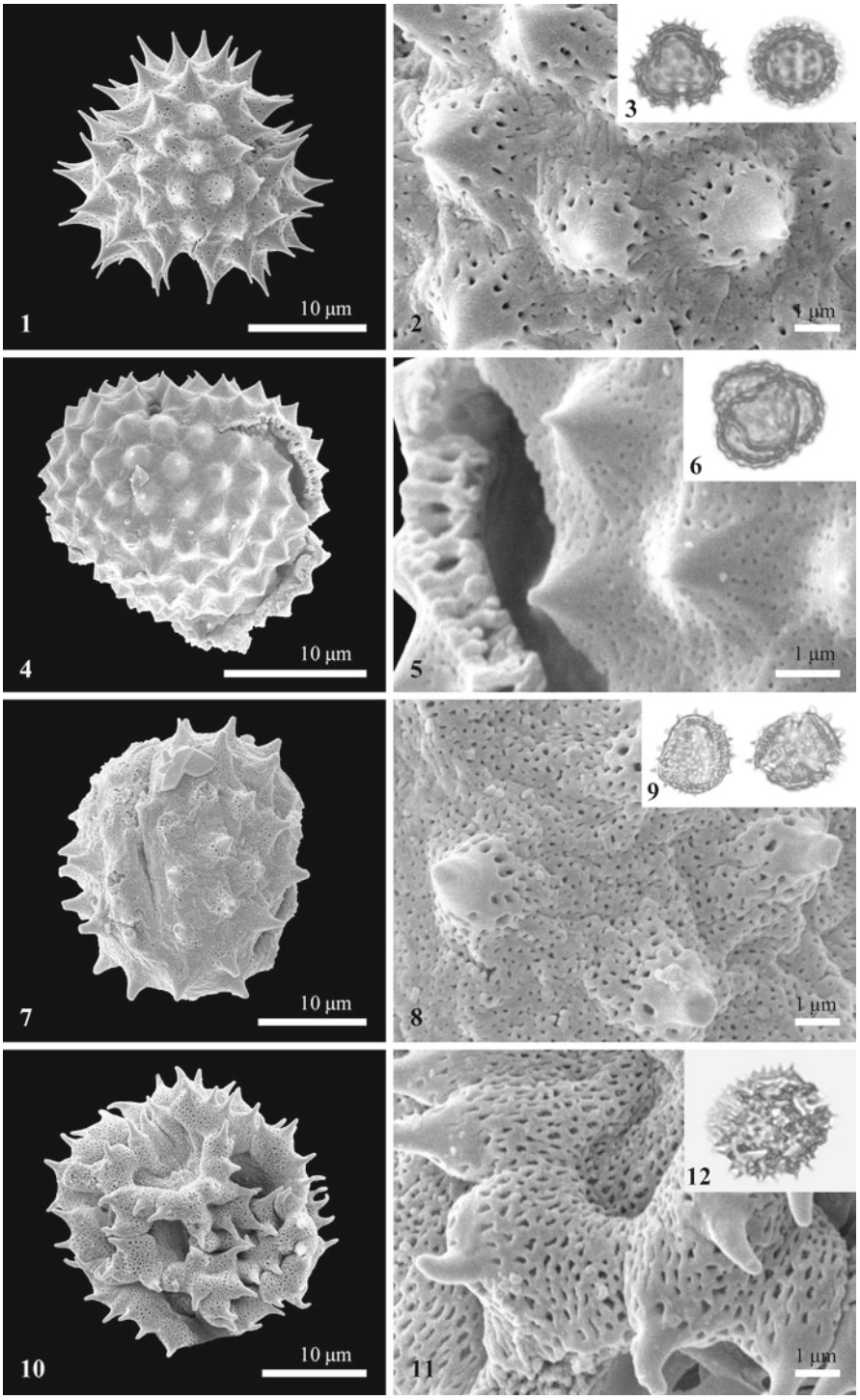



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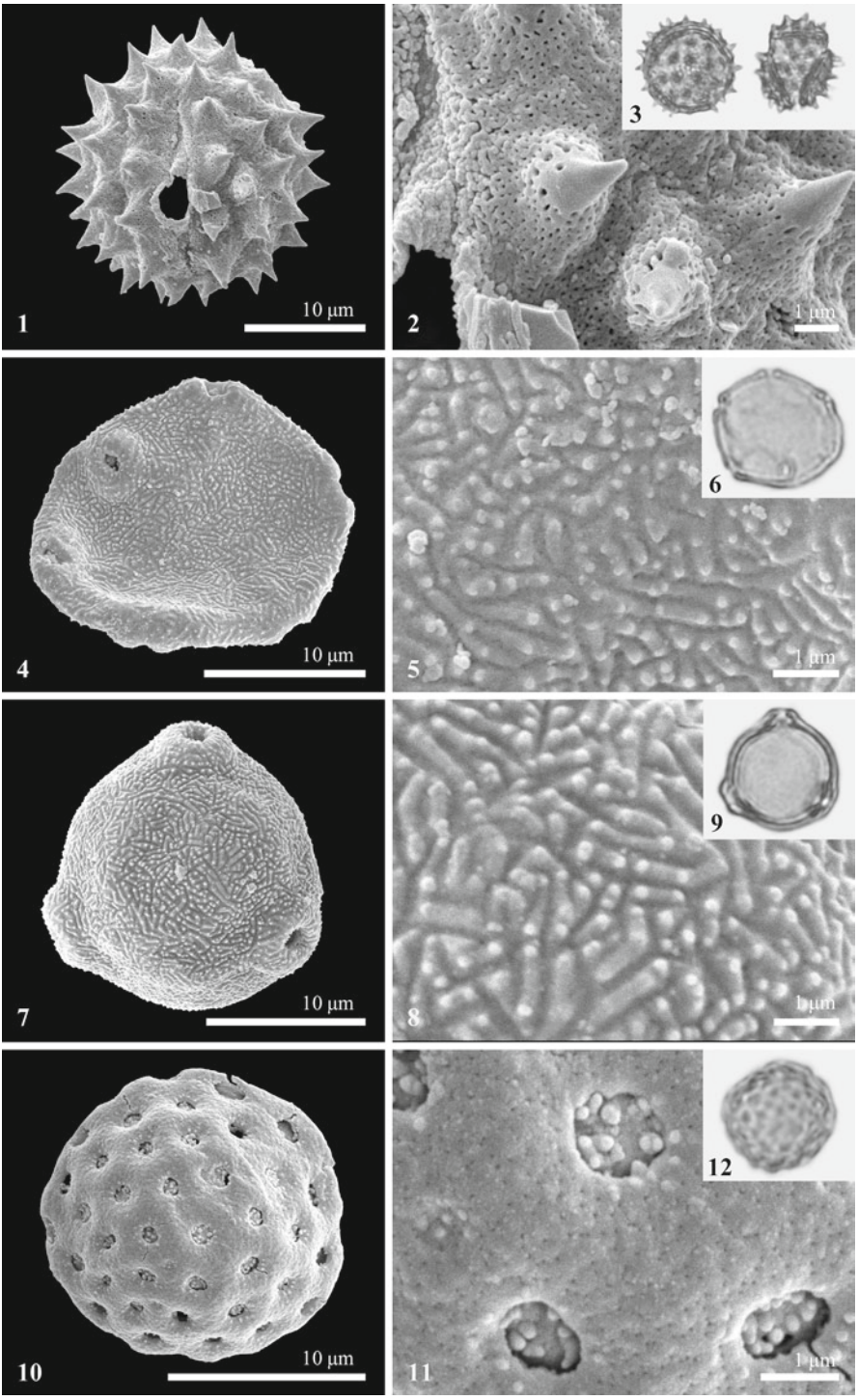



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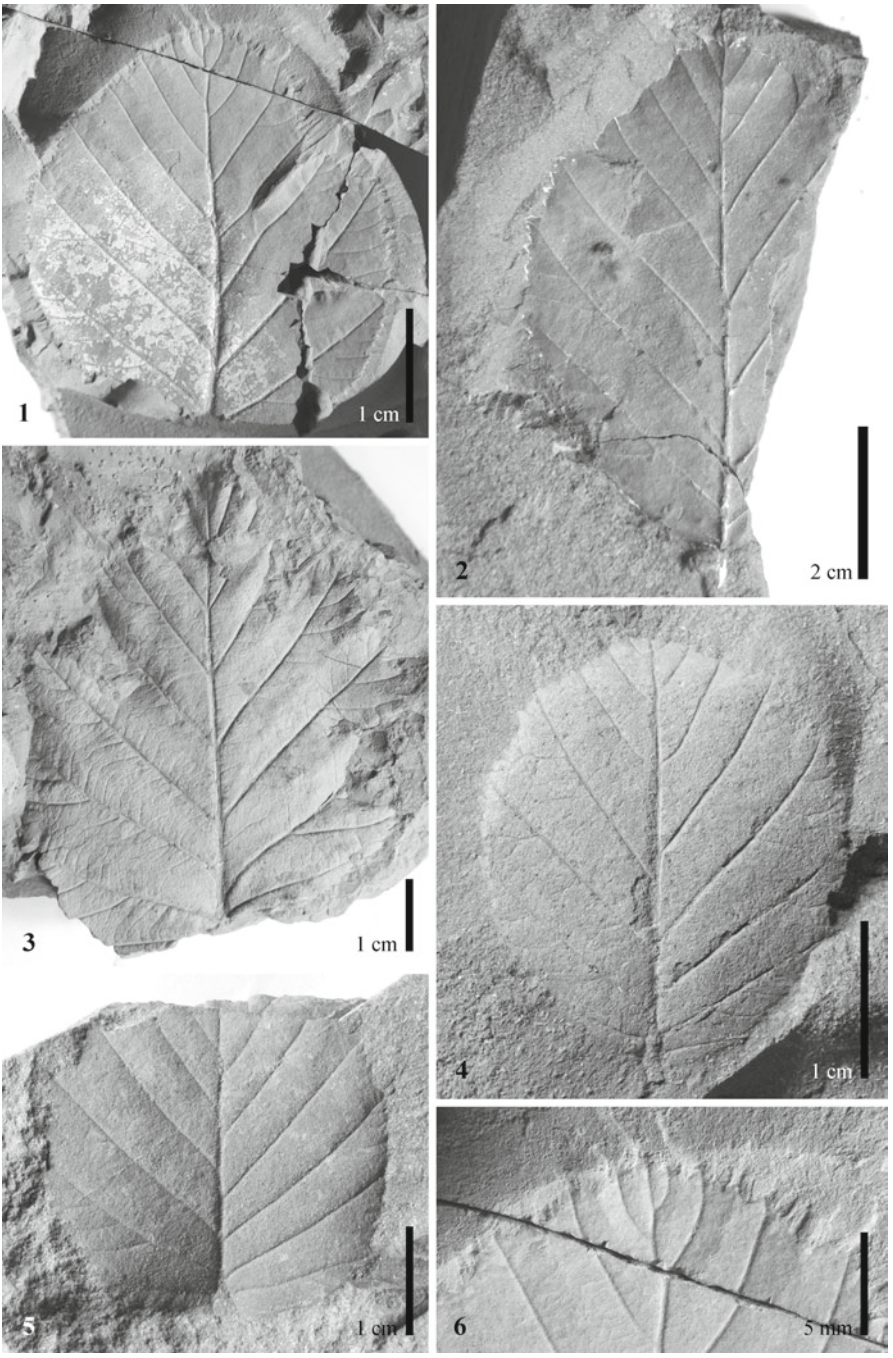



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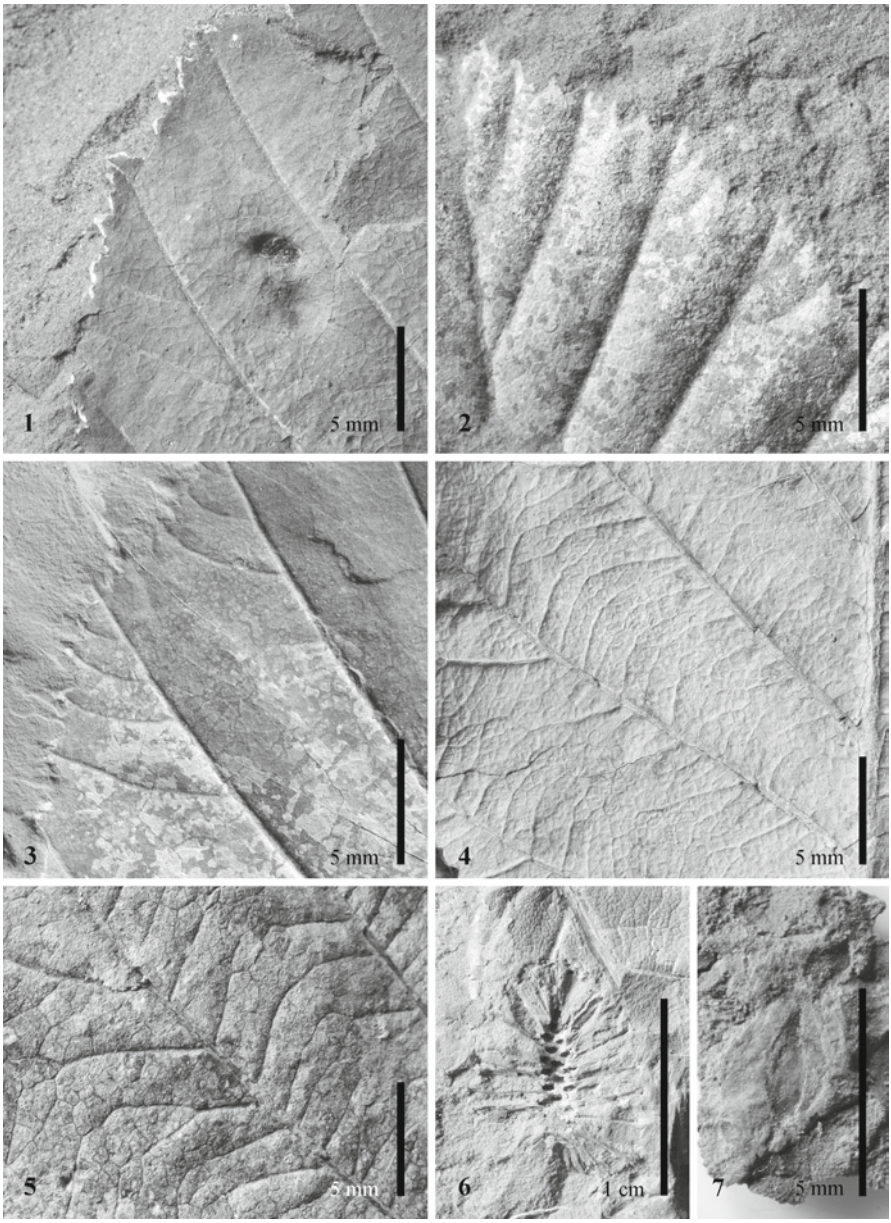



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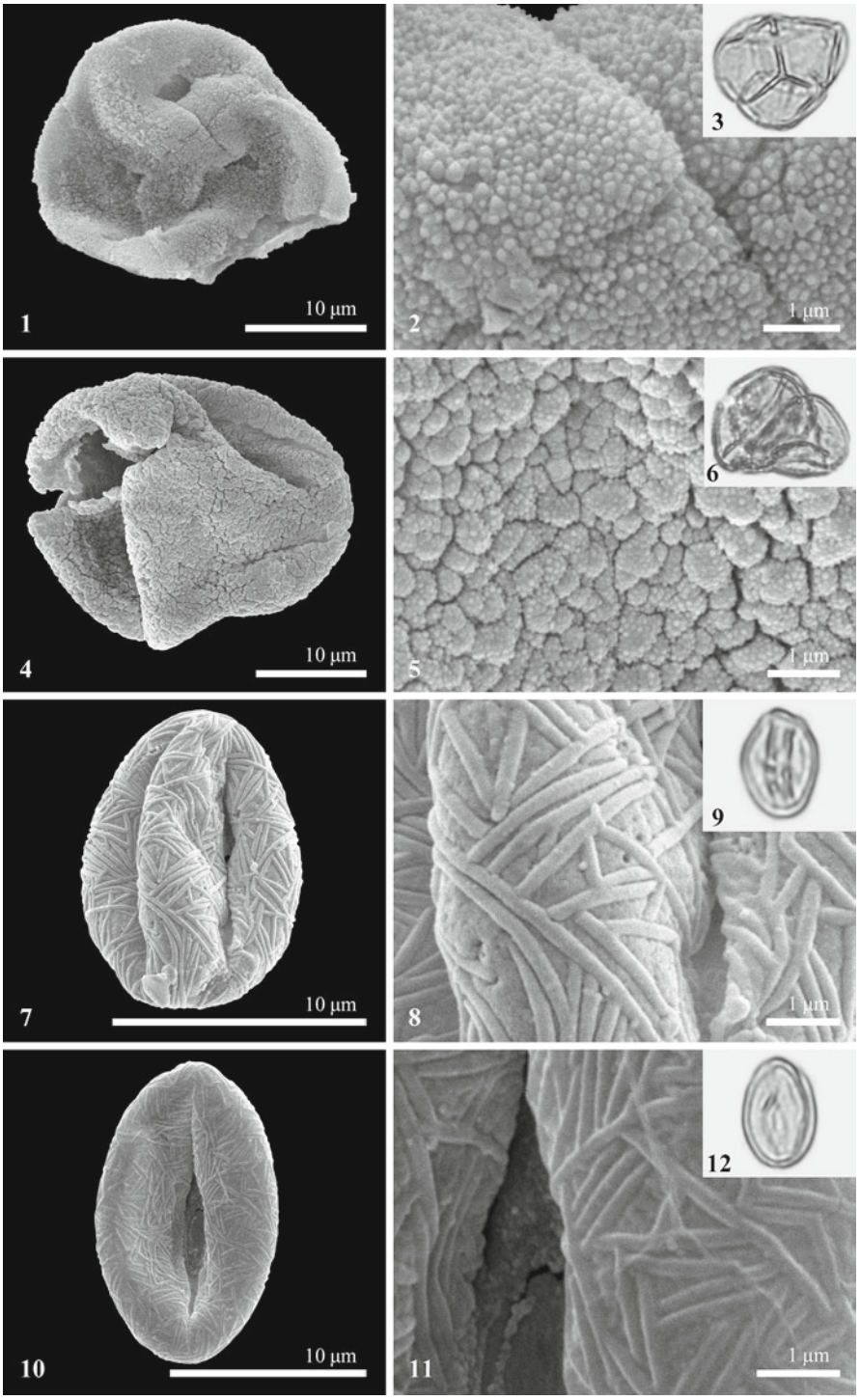



**Plate 11.38**




**Plate 11.39**

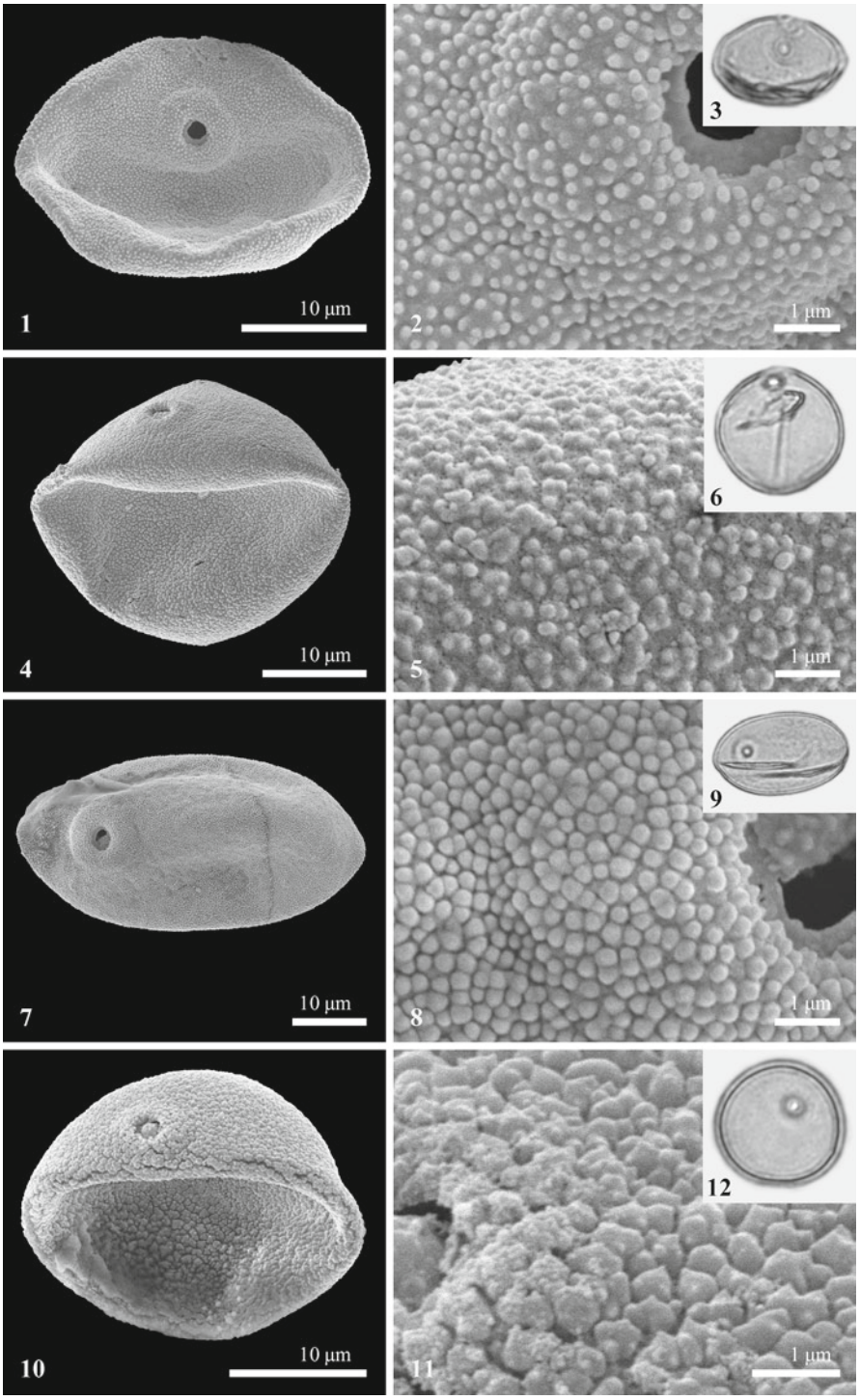



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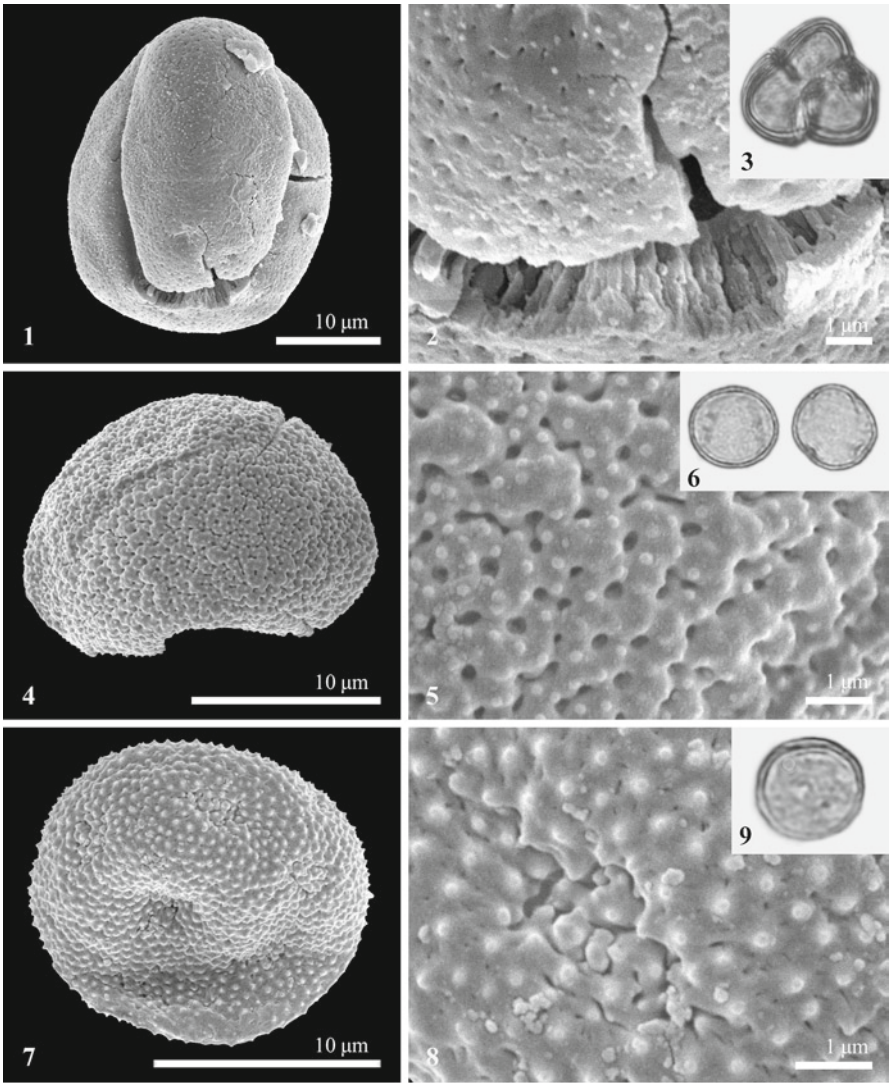



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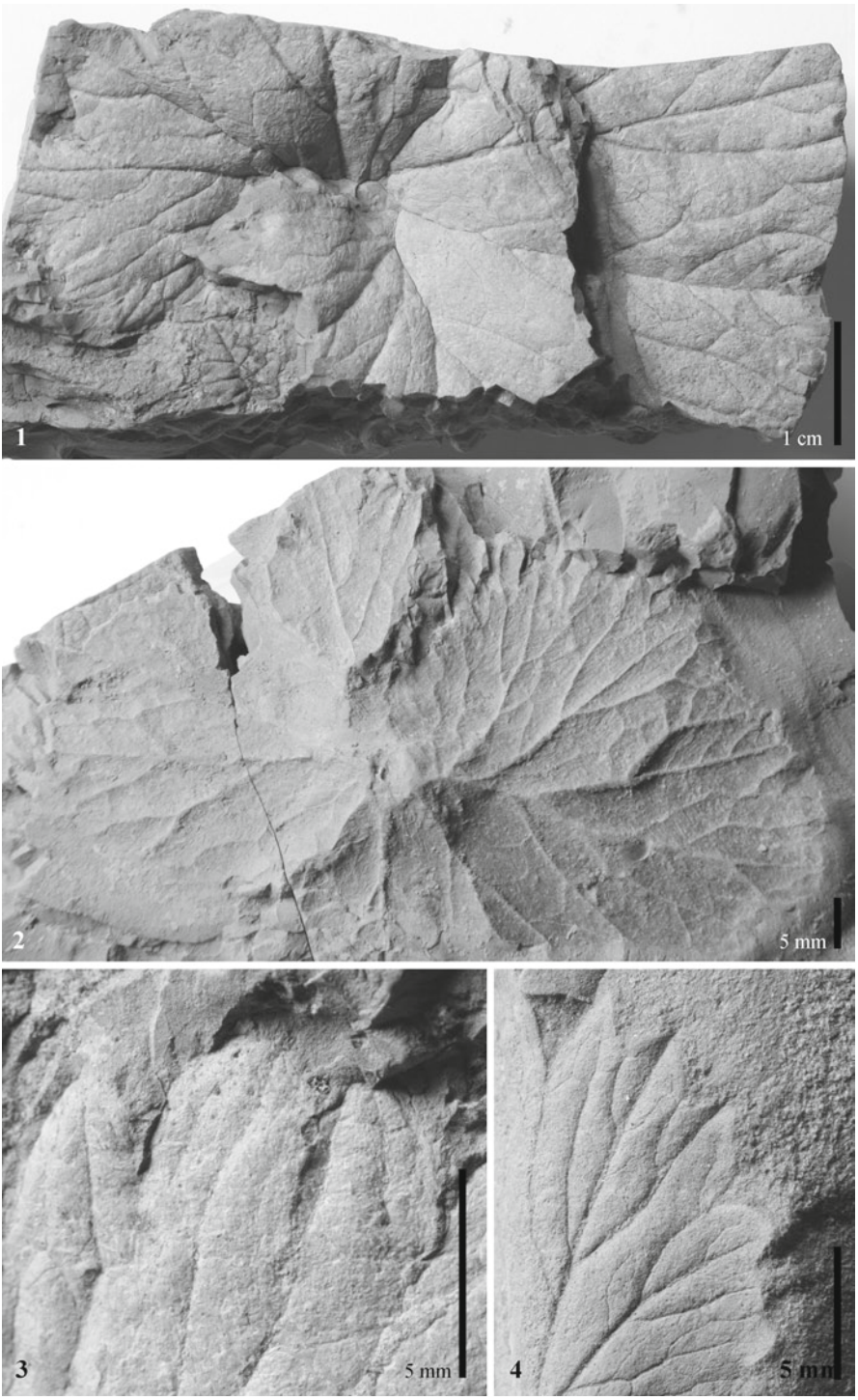



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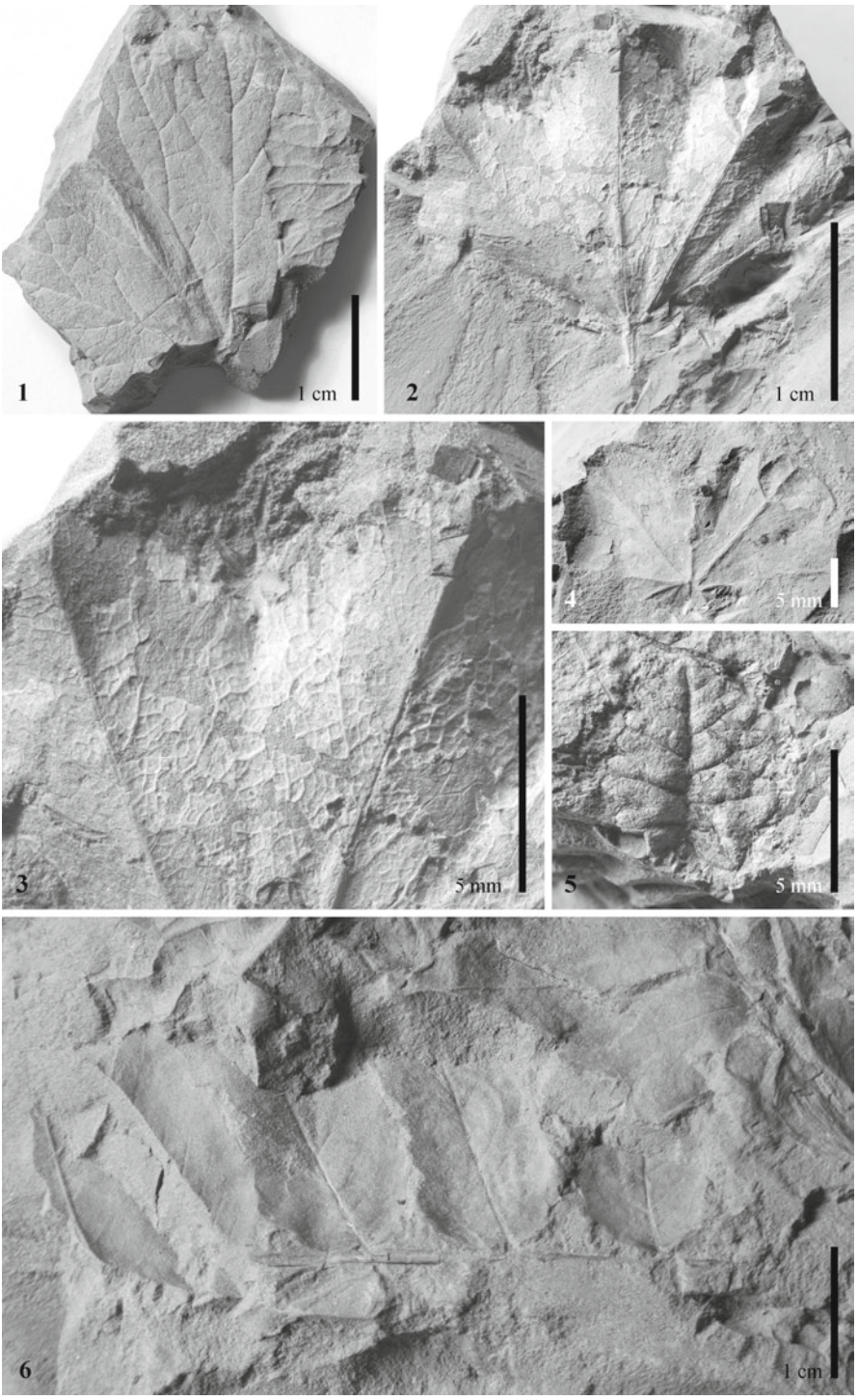



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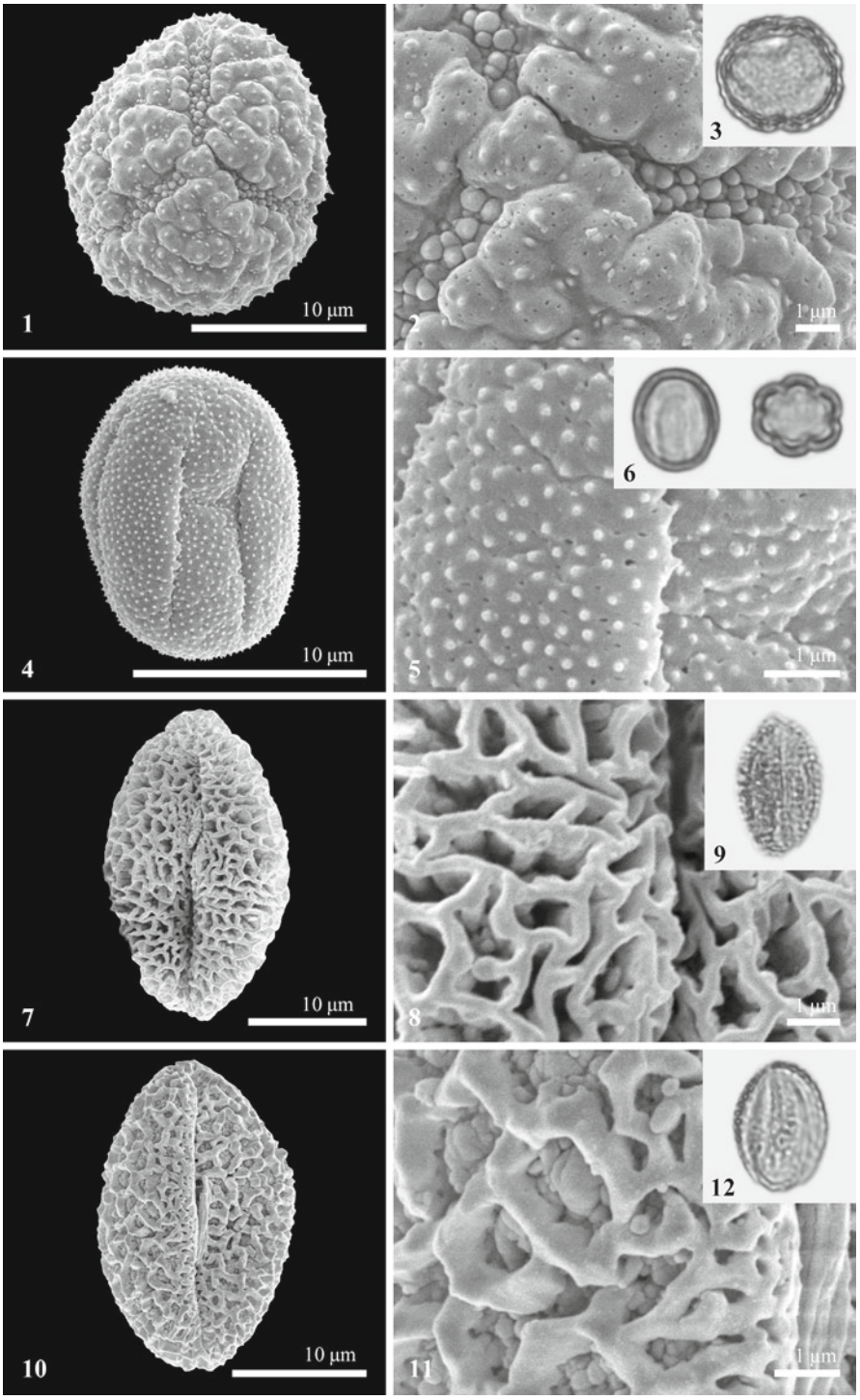



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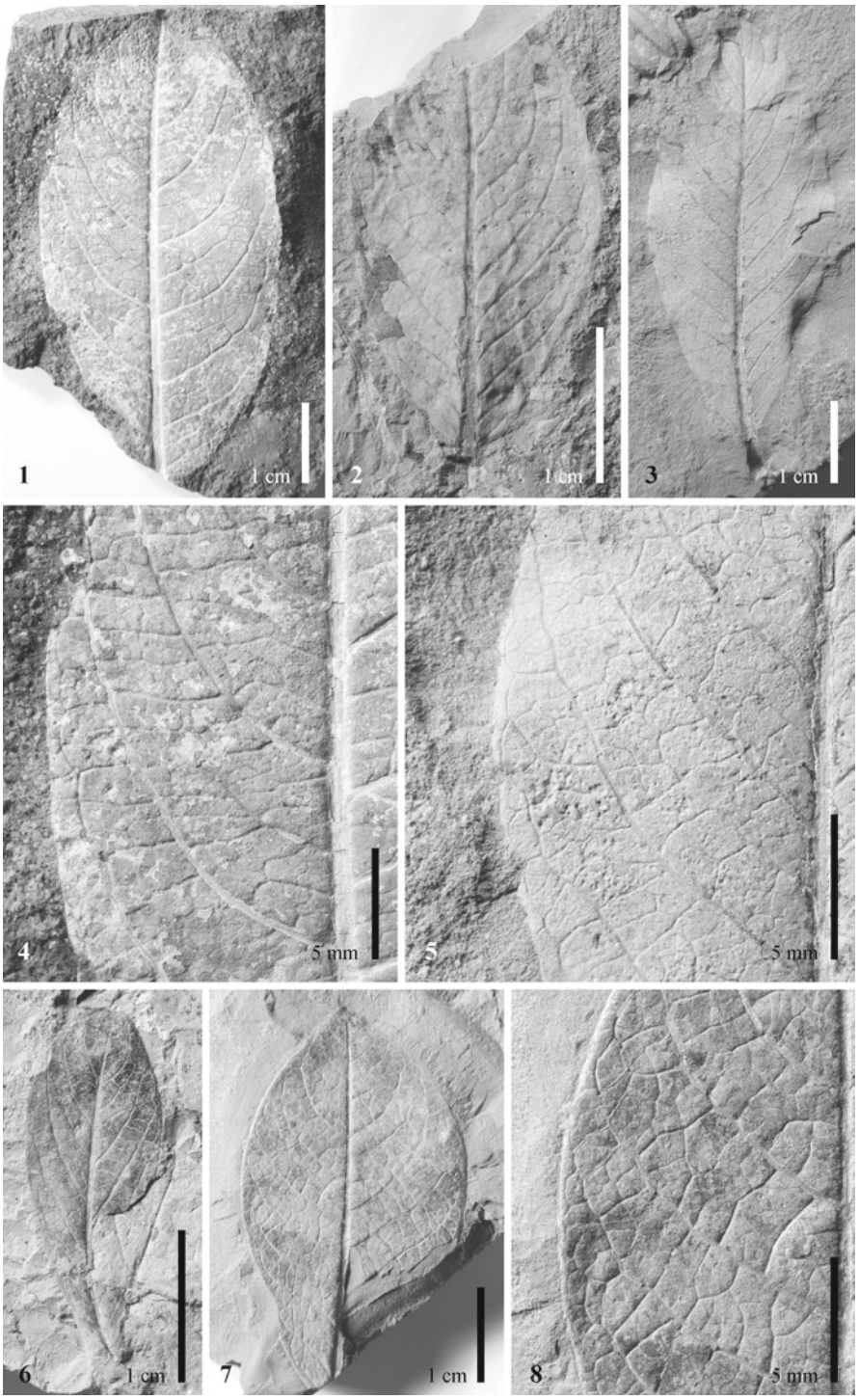



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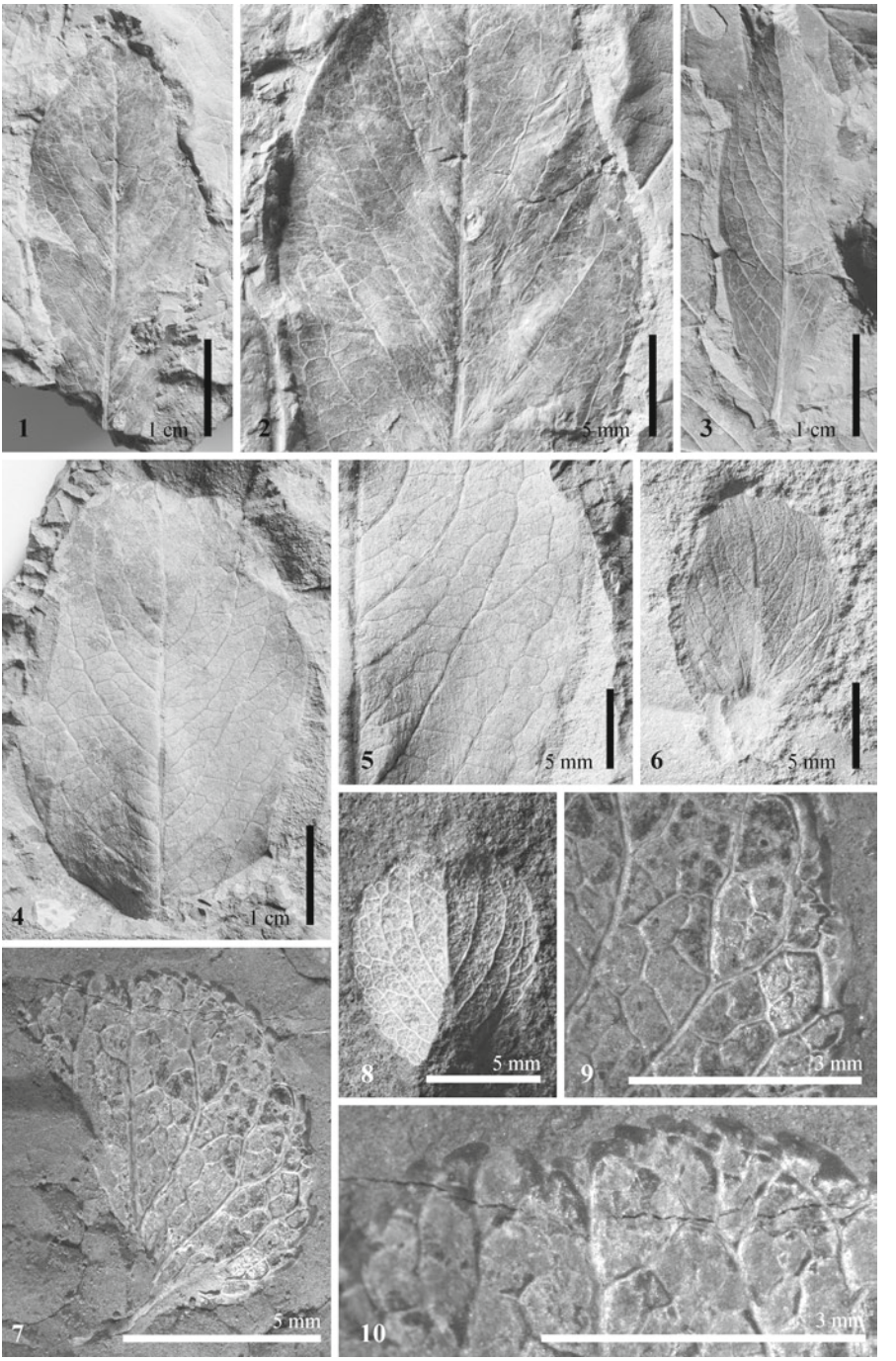



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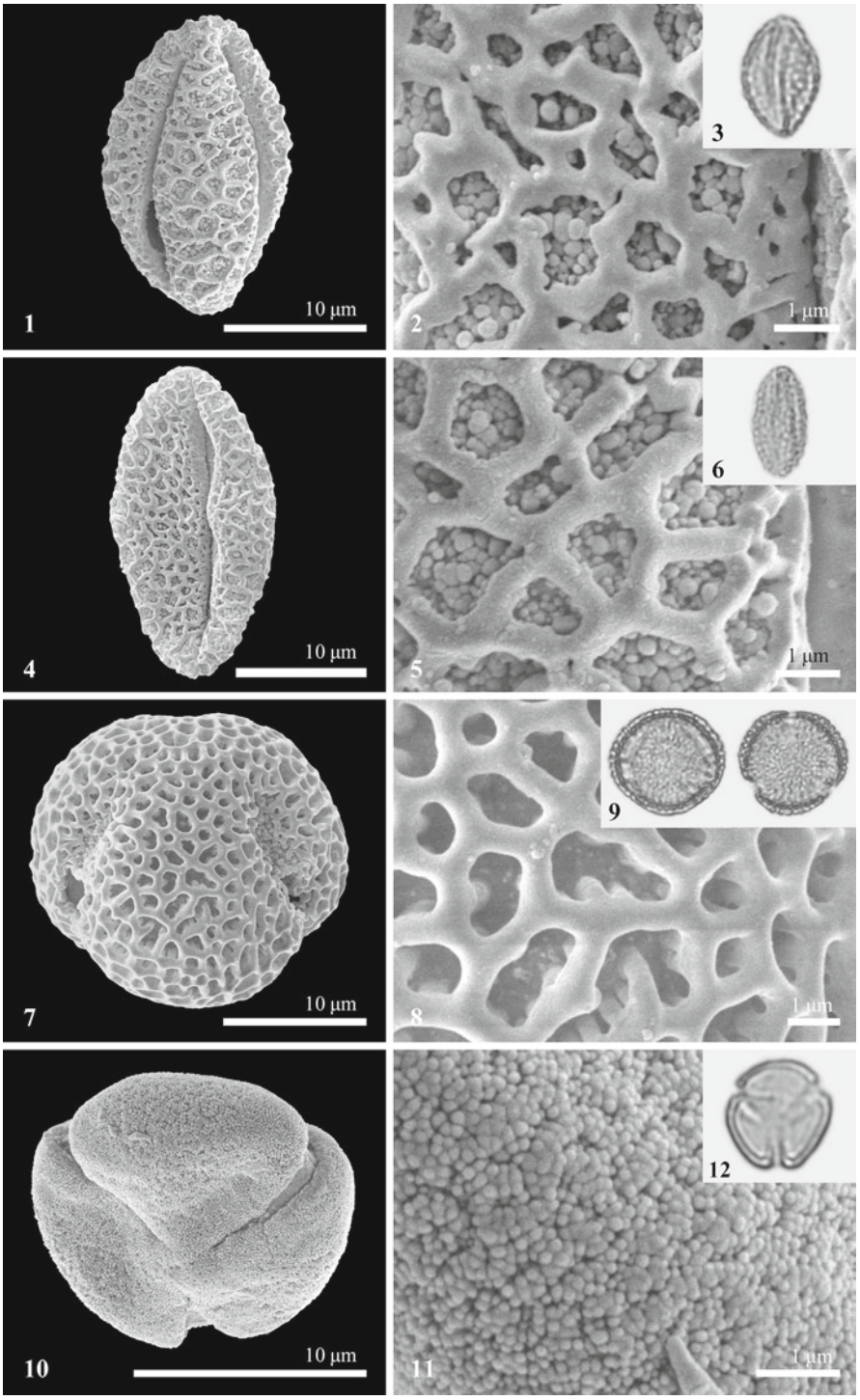



**Plate 11.47**

# Chapter 12
# The Biogeographic History of Iceland – The North Atlantic Land Bridge Revisited

**Abstract** Plants lacking long distance dispersal mechanisms required a functioning land bridge to colonize Iceland, a route provided by the North Atlantic Land Bridge (NALB). During the Cainozoic, the NALB, also referred to as the Thulean route, came into existence in the latest Paleocene and Early Eocene, but there has been considerable debate about the timing of its termination. The North Atlantic Land Bridge consisted of the well defined subaerial Greenland-Scotland Transverse Ridge. The individual parts of this ridge may have undergone markedly different subsidence histories during the Neogene. At the western end of the NALB, possible links between Greenland and North America are provided by the shallow bathymetric sill at the Davis Strait between southern Baffin Land and southwestern Greenland, and, alternatively, the more northern land connection between the Queen Elizabeth Islands and Greenland. In this chapter, we use evidence from different disciplines (geology, palaeontology, phylogeography), amended with a large new palaeobotanical data set emerging from the present study, to evaluate the history of the North Atlantic Land Bridge and its potential role for transatlantic plant migration during the Neogene.

## 12.1 Origin and Subsidence History of the North Atlantic Land Bridge (NALB)

### *12.1.1 The Greenland-Iceland and Iceland-Faeroe Parts of the NALB*

In the early Cainozoic, Greenland and Europe were close enough for the Iceland mantle plume (see Chap. 1) to sustain a subaerial transverse ridge, the Greenland-Scotland Transverse Ridge (GSTR; Fig. 12.1). During the course of the Neogene, the marginal regions of this ridge cooled and submerged. At present, the Greenland-Iceland portion of the GSTR is ca 280 km wide at its narrowest part. The continental shelf of East Greenland and the insular shelf of Iceland almost merge in the Denmark Strait. The water depths on the Greenland Shelf are 200–400 m, and 0–200 m on the Iceland shelf. These two shelves are separated by the 20–30 km wide and 600 m deep

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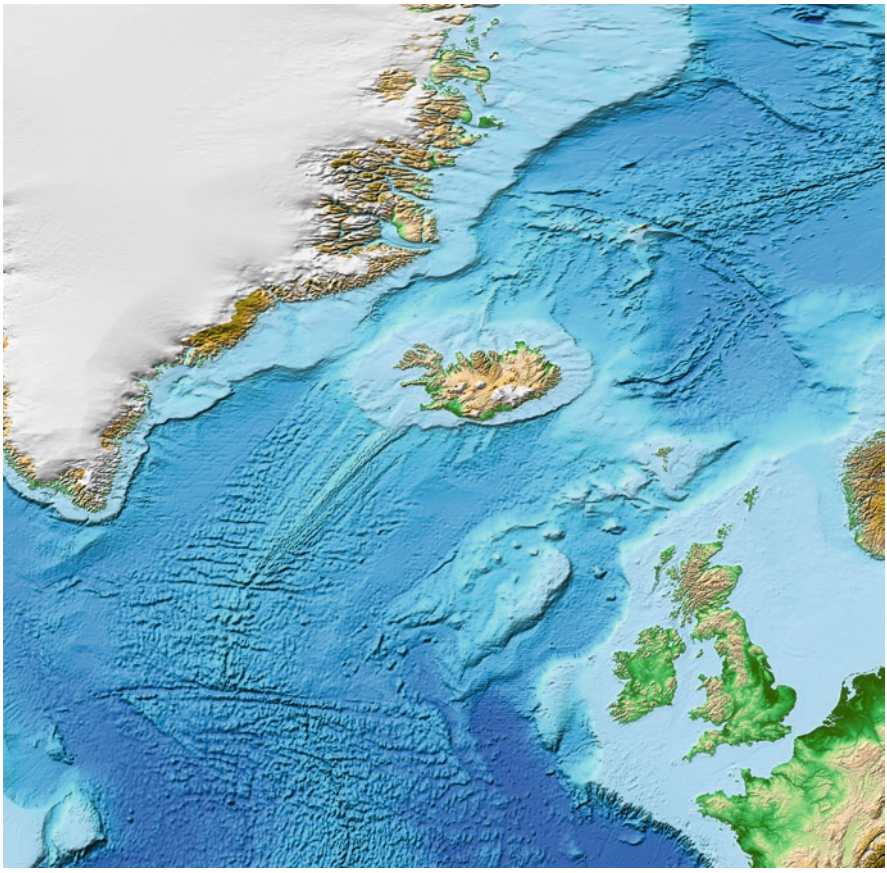


**Fig. 12.1** Bathymetric map of the northern North Atlantic showing the Greenland-Scotland Transverse Ridge (Picture courtesy NOAA, National Geophysical Data Centre)

Denmark Strait Channel (Larsen 1983). The Iceland-Faeroe portion of the GSTR is about 435 km long and the ocean depth is currently not more than 500 m. It is built from overthickened oceanic crust overlain by 0–400 m of marine sediments (Poore et al. 2006). The subsidence history of these two ridge parts is not entirely clear (Table 12.1). Using different subsidence models, Thiede and Eldholm (1983) and Poore et al. (2006) suggest that the Greenland-Iceland part of the GSTR may have become (partly) submerged after 18–15 Ma, whereas Poore (2008) calculated 10 Ma. According to Nilsen (1978), the ridge crest of the Iceland-Faeroe part of the GSTR would have sunk below sea level at about 14 Ma. Similarly, Eldholm et al. (1994) suggested that the lowest parts of the Iceland-Færoe part of the ridge would have submerged at 20 Ma, whereas higher parts of the crest would have remained subaerial until ca 10 Ma. Thiede and Eldholm (1983) suggested that isolated peaks of the GSTR may have remained subaerial until as late as the Pliocene. Strauch (1970, 1972, 1983) argued for a continuous land bridge until the Pliocene based on palaeontological evidence from a large number of genera of marine molluscs.

**Table 12.1** Suggested ages for the timing of subsidence of different parts of the North Atlantic Land Bridge

| Reference | Davis Strait | Greenland-Iceland Ridge (Denmark Strait) | Iceland-Faeroe Ridge | Faeroe-Scotland Ridge (general) |
|---|---|---|---|---|
| **Geological evidence** | | | | |
| Nilsen (1978) | | | Ridge crest at 14 Ma | |
| Thiede and Eldholm (1983) | | After 15–18 Ma | Main ridge platform not before Middle Miocene; highest peaks not later than Pliocene | 40–50 Ma [uncertain ages]; possibly falling dry during certain periods |
| Srivastava and Arthur (1989) | Emergent until ~30 Ma | | | |
| Eldholm et al. (1994) | | Boundary Middle to Late Miocene | About 20 Ma; shallower parts about 10 Ma | Middle Eocene |
| Stoker et al. (2005) | | | | No overflow proven before Early/mid-Miocene; from Early/mid-Miocene to earliest Pliocene the Faroe Conduit forms a narrow sea way |
| Poore et al. (2006) | | After 15–18 Ma | After 15–18 Ma; 100–200 m below sea level by 12 Ma | Throughout the Cainozoic |
| Poore (2008), Chap. 6 | | At about 10 Ma | Between 10 and 20 Ma | Late Eocene |
| **Palaeontological evidence** | | | | |
| Strauch (1970, 1972, 1983) [marine molluscs] | Since Palaeogene | Boundary Pliocene/Pleistocene | Boundary Pliocene/Pleistocene | Boundary Pliocene/Pleistocene |
| Berggren and Schnitker (1983) [benthic foraminifera] | | | | Before mid-Eocene |
| McKenna (1983a, b) [vertebrates] | Eocene | Oligocene/Miocene | Oligocene/Miocene | Early Eocene |
| Tiffney (1985, 2000) [plant fossils] | Late Eocene | | | |
| Ramsay et al. (1998) [benthic foraminifera] | | After 18–13 Ma | After 18–13 Ma | After 18–13 Ma |
| PRESENT STUDY [plant fossils] | | After 6 Ma | After 10 Ma | After 10 Ma |

### *12.1.2 The Greenland-North American Connection (Davis Strait)*

The southwestern part of Greenland is connected with Baffin Island via a shallow bathymetric sill at the Davis Strait, which is a continuation of the mid-Labrador ridge. The Davis Strait is ca 325 km wide at its narrowest and 400–800 m deep (Srivastava 1983). The subsidence history of this ridge is difficult to establish because the nature of the crust that underlies it is complex; it is mainly built up of continental crust with a narrow zone of oceanic crust (Funck et al. 2007). Srivastava and Arthur (1989) calculated that this ridge could not have subsided below sea-level before 30 Ma based on the spreading age of normal oceanic floor of 60 Ma and a present mean depth of 500–750 m. Although Srivastava and Arthur (1989) based their model on the assumption that the Davis Strait was underlain by oceanic crust, their estimate appears to be more or less correct. Piasecki (2003) showed that sediments in this area are of fully marine origin throughout the Neogene. Hence, this link appears not to have played a role for the Neogene Thulean route (cf. Strauch 1970; Denk and Grimm 2009).

### *12.1.3 The Faeroe-Scotland Part of the NALB*

The Faeroe-Scotland part of the Greenland-Scotland Transverse Ridge is underlain by continental crust and thus followed a different mode of evolution than the remaining parts of the GSTR (Stoker et al. 2005). Features such as the Faeroe-Shetland Channel have traditionally been thought to have remained submerged since the Early Cainozoic (Table 12.1), but may have been above sea level during certain periods (Thiede and Eldholm 1983). Miller and Tucholke (1983), Davies et al. (2001), and Poore (2008; Fig. 12.2), among others, used sediments, erosional surfaces, and unconformities and percentage of Northern Component Water (NCW) inferred from benthic foraminifera isotope ratios to suggest southwards-flowing NCW transport over the Faeroe-Scotland part of the GSTR in the Early Cainozoic. In contrast, Stoker et al. (2005; Fig. 12.3) argued that this part of the GSTR remained subaerial or at least constituted shelf areas between 25 and 15 Ma and that this link was interrupted by a narrow Faeroe Channel only after the Early/Middle Miocene, with large subaerial or shelf areas lasting until the earliest Pliocene.

## 12.2 Explanations for Cainozoic Plant Migration to Iceland

According to Nilsen (1978) and McKenna (1983a, b) the timing of early colonization of Iceland cannot be established exactly. The closest species-level relatives of taxa recovered from 15 Ma plant-bearing sedimentary rocks of Iceland were either

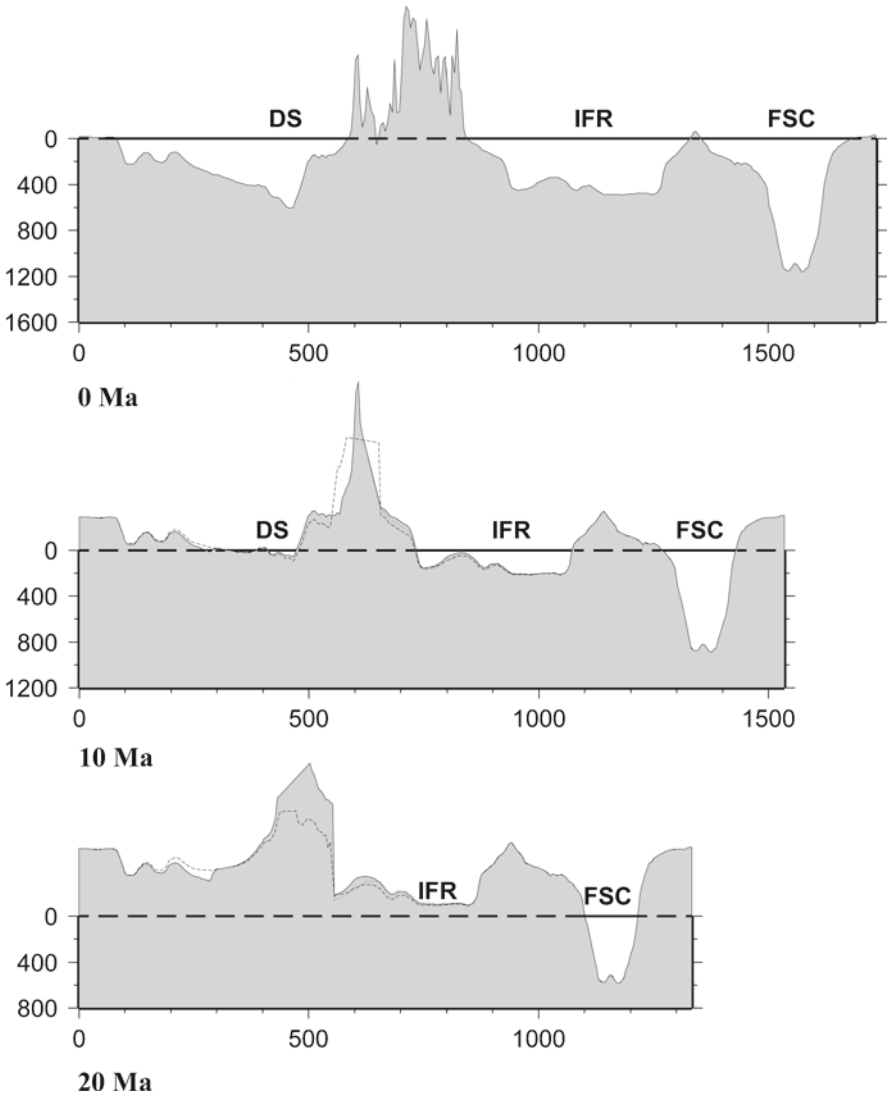



**Fig. 12.2** Subsidence history of the Greenland-Scotland Transverse Ridge. The calculation accounts for plate cooling and spreading but not for sediment accumulation on the ridge over the past 20 Ma; nor does the model account for the different type of crust in the Faeroe Scotland area and hence is not reliable for this region. *DS* Denmark Straits, *IFR* Iceland-Faeroe Ridge, *FSC* Faroe-Shetland Channel. Water depths (m) and width of GSTR (km) are indicated (Modified after Poore 2008)

in North America, Greenland or Europe (cf. Grímsson and Denk 2007). "Subaerial Iceland began to form at about the time of marine magnetic anomaly 24, at about 54 Ma, and appears to have remained connected to Greenland until sometime in

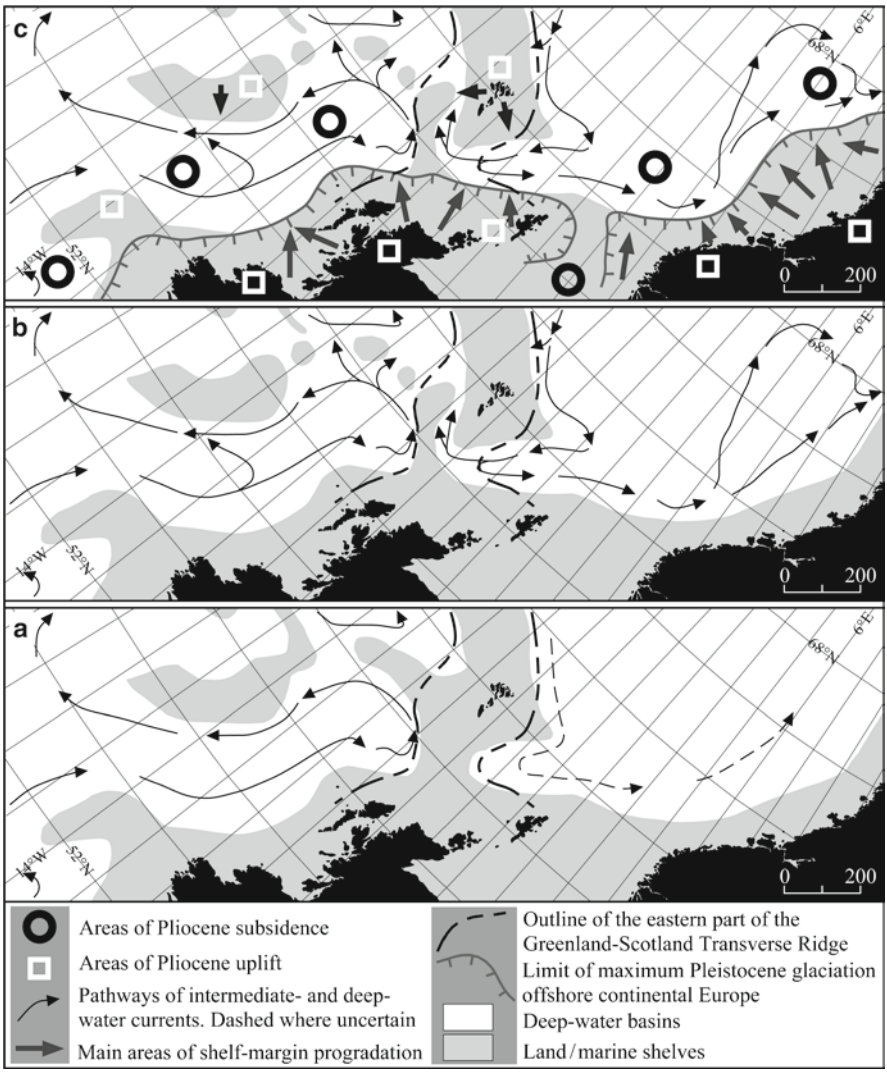



**Fig. 12.3** Schematic reconstructions showing the palaeogeographic history of the eastern part of the Greenland-Scotland Transverse Ridge, part of the NALB. **a** Late Oligocene to Early Miocene. **b** Early/mid-Miocene to earliest Pliocene. **c** Early Pliocene to Holocene. Scale bar in km (Modified after Stoker et al. 2005)

the Miocene. It might therefore be expected that Iceland once possessed a biota whose origin from a continent could have been, except for later dispersals, earlier than the oldest rock now preserved above sea level in Iceland" (McKenna 1983b).

McKenna (1983a, b) proposed an "escalator counterflow" model to account for the early colonization of Iceland. The model predicts that plants could have migrated to Iceland at any time after the Iceland mantle plume had started to sustain a subaerial Greenland-Scotland Transverse Ridge in the early Cainozoic. Since it takes approximately 15–20 Ma of lateral transport for land formed above the centre of the mantle plume (hotspot) to sink below sea level (McKenna 1983b; cf. Steinþórsson, 1981), organisms would have to move towards the plate boundary at the same rate as new crust is created – perhaps a centimetre or a few centimetres per year. McKenna (1983a, b) apparently took it for granted that Iceland at 15 Ma was an isolated island.

Using the macrofossil record, Grímsson and Denk (2007) analysed dispersal modes of plants that arrived in Iceland at different times. Plants found in the oldest plant-bearing sedimentary rocks (15 Ma, see Chap. 4) display different modes of dispersal, among which dischory (where normally fairly large diaspores are dropped near the mother plant) is as common as long-distance wind dispersal, but much less common than wind dispersal over short distances (Figs. 12.4 and 12.5). Overall, this strongly suggests that Iceland was not an isolated island at the time when it was colonized. However, it is very likely that the early colonization of Iceland occurred prior to the deposition of the oldest known plant bearing sedimentary formations in Iceland. Indeed, many taxa recorded for the Middle Miocene formations in Iceland were common elements in Oligocene to Miocene sediments from North America and western Eurasia (Hably et al. 2000). Based on the consensus of a variety of geological and palaeontological studies (Table 12.1) it seems highly probable that most of the GSTR was subaerial until at least the Middle Miocene (ca 15 Ma). This would not require an escalator counterflow model as suggested by McKenna (1983a, b) but rather suggests colonization via an unbroken land bridge from the adjacent continents for plants recorded in the oldest sedimentary rocks.

Tiffney (1985, 2000), in the absence of fossil data from Neogene terrestrial sediments in the North Atlantic, acknowledged data from phylogeographic studies and suggested a stepping stone model via a chain of islands to explain possible migration to Iceland in the later parts of the Cainozoic. Tiffney (1985) summarized palaeobotanical data regarding the NALB in the early Cainozoic. McKenna (1983a) and Tiffney (1985) did not consider the possibility of a persisting NALB after the Eocene. In later papers, Tiffney (2000) and Tiffney and Manchester (2001) discuss the possibility of a persisting bridge or closely-spaced island chain through the Middle Miocene. More recently, Tiffney (2008) summarized recent palaeobotanical and phylogeographic results relevant for northern hemisphere biogeography. According to this, a growing body of evidence from different disciplines is indicative of a functioning NALB into the late Cainozoic. In the following section, we provide new data from the palaeobotanical record in Iceland corroborating this view and allowing more precise statements about the possible termination of the NALB.

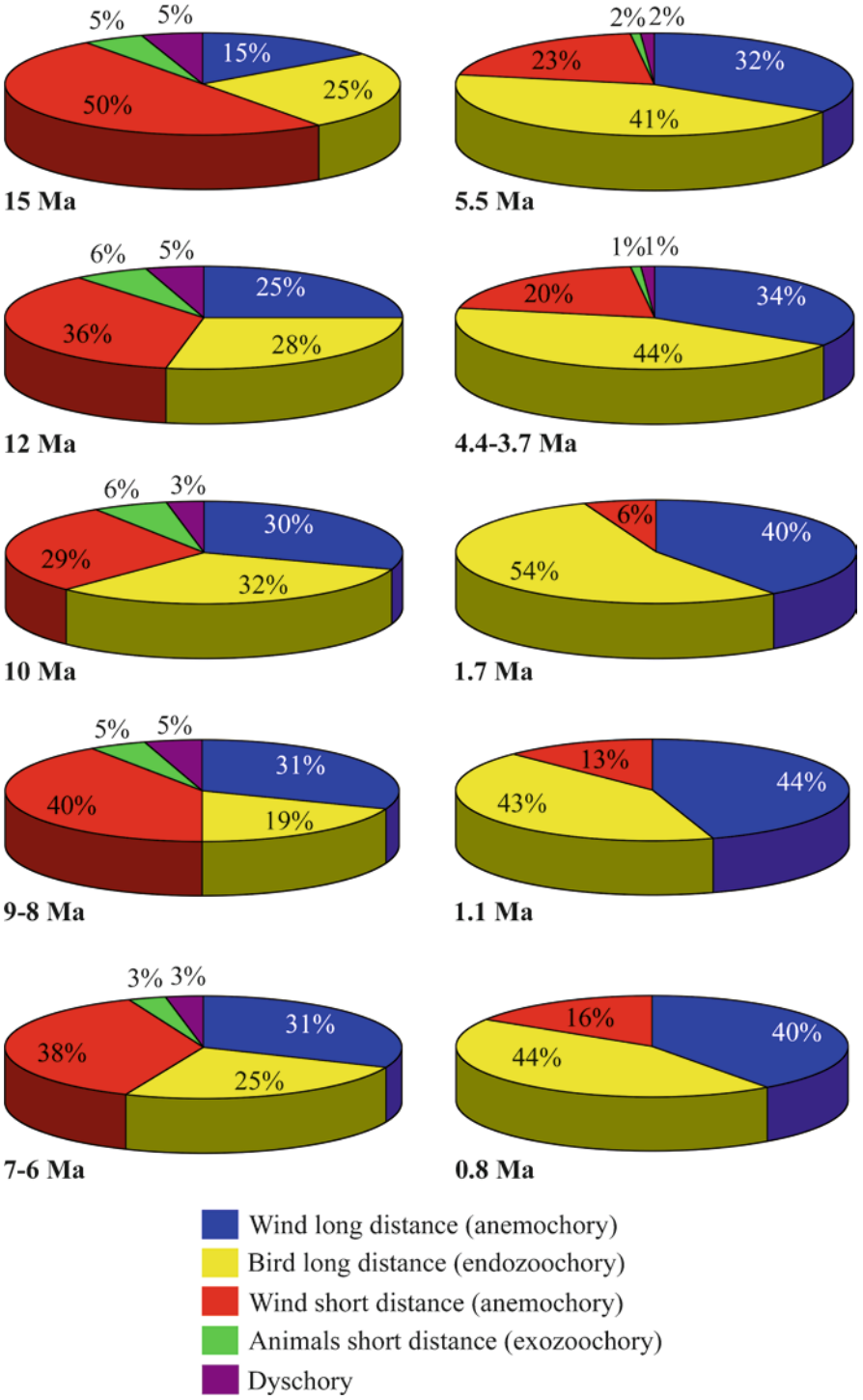



**Fig. 12.4** Dispersal modes for taxa recorded from 15 to 0.8 Ma plant bearing sedimentary rock formations in Iceland. Note a continuous increase in long distance wind dispersal and the loss of taxa with short distance dispersal by animals and dyschory after 3.7 Ma

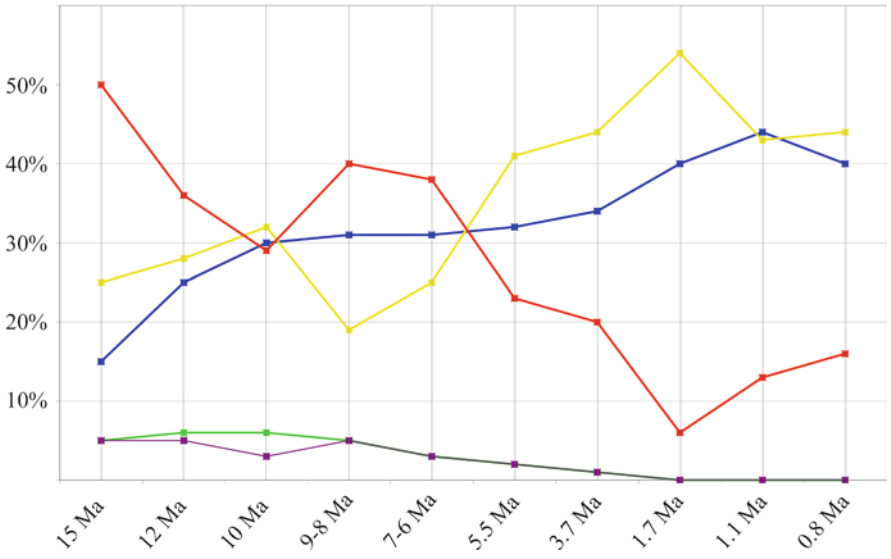



**Fig. 12.5** Summation of changes in dispersal modes between 15 and 0.8 Ma. Note the increase in long distance dispersal by wind (*blue*) and birds (*yellow line*). See Fig. 12.4 for legend

## 12.3 Fossil Evidence

As mentioned above, it is unclear at which time plant taxa recorded in the 15 Ma formation (Chap. 4; Appendix 12.1) first arrived in Iceland. Based on the modes of dispersal found in these taxa, however, it is clear that when this happened, Iceland was part of a functioning land bridge, i.e. a mostly unbroken GSTR (cf. Fig. 12.1) and a passable continuation via Greenland to North America. Elements migrating from North America would have crossed over to Greenland via the Queen Elizabeth Islands (cf. Grímsson and Denk 2007; Denk and Grimm 2009; Denk et al. 2010) and probably not via the Davis Strait (Srivastava and Arthur 1989). The necessity of a continuous land bridge is underscored by the large number of plant taxa with dyschory (e.g. *Aesculus*) and wind (or rarely water) dispersal over short distances (see Table 4.1, Chap. 4; Figs. 12.4 and 12.5). Elements such as *Fagus friedrichii* Grímsson and Denk and *Tetracentron* quite likely arrived from the west (Grímsson and Denk 2007; Grímsson et al. 2008; Denk and Grimm 2009), while most other taxa are not indicative of any particular migration route because they have a good fossil record both in North America and Europe (e.g. *Cercidiphyllum*; Grímsson and Denk 2007; Grímsson et al. 2007).

In the 12 Ma formation, a number of taxa occur for the first time. Many of these taxa are bird-dispersed over long distances, and thus would not require an intact land bridge for dispersal (*Ephedra*, *Comptonia*, *Liriodendron*, *Sassafras*, and *Smilax* among others; Chap. 5). However, several taxa seem unlikely to have reached

Iceland by crossing a wide ocean or even by island hopping (*Alnus gaudinii* (Heer) Knobl. and Z. Kvaček; *Carya*, *Corylus*; Table 5.1, Chap. 5; Figs. 12.4 and 12.5). *Alnus gaudinii* is most similar to some Asian Minor and East Asian modern species (Hably et al. 2000; Denk et al. 2005) and has a rich fossil record in Miocene floras of Europe (Kvaček et al. 2002) indicating migration between Iceland and Europe.

The 10 Ma formation is characterized by a large number of herbaceous taxa, most of which are absent from the older formations. Most of these plants could have reached Iceland by birds (endozoochory; see Table 6.1, Chap. 6; Figs. 12.4 and 12.5). In contrast, a number of tree taxa appearing for the first time in the 10 Ma Tröllatunga-Gautshamar Formation would have required a more or less continuous land bridge (*Larix*, *Pseudotsuga*, and *Cyclocarya*). These plants have winged disseminules that are dispersed by wind over short distances. Even stronger evidence for a physical link between Europe and Iceland between 12 and 10 Ma comes from the extinct genus *Trigonobalanopsis* (Fagaceae) that appears to have been present in Iceland from 10 to 3.7 Ma (Appendix 12.1). This genus is an important element in Miocene floras of Europe (Kvaček and Walther 1989; Walther and Zetter 1993; Zetter 1998) but has not been recorded from North America. Its pollen is highly distinctive when investigated under the scanning electron microscope (Walther and Zetter 1993; Chap. 6, Plate 6.27). In view of the absence of *Trigonobalanopsis* in North America the genus most likely migrated to Iceland from Europe.

The floras of the 9–8 Ma formation are overall less species rich (see Chap. 7). Among the taxa that appear for the first time, most are wind dispersed (spore-producing plants, Asteraceae; Fig. 12.4) or dispersed by birds over long distances (e.g. *Cornus* sp., *Ilex* sp. 2). Again, however, two species within the Fagaceae, *Quercus* sp. 1 and *Fagus gussonii* Massalongo, must have reached Iceland on more or less continuous land. While *Quercus* sp. 1 represents a general type found in various Eurasian and North American white (and red) oaks (Denk et al. 2010), *Fagus gussonii* is endemic to Miocene sediments of southern Europe (Greece, Italy, Spain) and Iceland (Grímsson and Denk 2005) suggesting interchange with Europe. This record also provides the latest evidence for migration on land between Europe and Iceland (between 10 and 9–8 Ma).

In the 7–6 Ma formation, new elements indicative of an active land bridge are almost absent (Table 8.1, Chap. 8; Fig. 12.4). This may partially be due to the fact that the sedimentary rocks from this formation were less suitable for palynological studies than samples from the other formations, resulting in a rather limited palynological record. One exception is *Populus* sp. B which is closely similar to Middle Miocene and Oligocene *Populus* described from Central Europe, Siberia and Alaska (see Chap. 8). Assuming that this distinct type of *Populus* arrived in Iceland after 9–8 Ma and in view of its scanty fossil record it is impossible to say whether it migrated to Iceland from the west or the east. The biogeographic scenario here would be similar to the one discussed for *Tetracentron* (Grímsson et al. 2008) and *Pseudotsuga* (Denk et al. 2005). Water plants that occur for the first time in the 7–6 Ma formation (e.g. *Ceratophyllum* and *Myriophyllum)* are dispersed by ducks, among others (long-distance endozoochory; Ridley 1930).

The latest Miocene 5.5 Ma formation contains few biogeographically informative elements, among them *Quercus* sp. 2. This markedly distinct pollen type unambiguously relates to North American white (and to a lesser degree red) oaks (Denk et al. 2010). Similar types of dispersed oak pollen are known from East Asian Miocene sediments (Liu et al. 2007) but are missing from Europe (R. Zetter, pers. obs.). Thus, this element points to migration via a subaerial link – possibly from a southern Greenlandic population – to Iceland from the west as late as between 7–6 and 5.5 Ma.

The younger formations exclusively yield plant taxa that are dispersed over long distances by wind or birds (Fig. 12.4; see also Chaps. 10 and 11). One interesting exception may be *Euphorbia*. Some species of euphorbs are known as sea-dispersed (Ridley 1930). However, according to Mabberly (2008) *Euphorbia* is dispersed by ants, birds, and wind.

## 12.4 Phylogeographic Evidence

Over the last two decades a considerable number of molecular phylogenetic studies have been published that made use of mutation rates to infer divergence times for disjunct northern hemisphere taxa. Some of these studies provide evidence for a functioning NALB during various times of the Cainozoic based on biogeographical patterns of taxa with an eastern North American-European disjunction that are not dispersed over long distances (e.g. *Corylus*; Whitcher and Wen 2001). Others make general statements about the land bridges (NALB, Bering land bridge) involved in establishing intercontinental disjunctions in the course of the Cainozoic. The revised plant fossil record of late Cainozoic terrestrial sediments from Iceland (Chap. 3) provides an important means for evaluating molecular based biogeographic studies using only modern taxa.

Whitcher and Wen (2001) analysed modern species of *Corylus* and, based on nucleotide differences, inferred a Pliocene to Pleistocene divergence age for European and eastern North American members of subsection *Corylus*. These authors suggested wind- or bird-dispersal over an already substantially widened North Atlantic Ocean to achieve this young divergence. Based on palaeobotanical evidence, *Corylus* was present in Iceland from 12 to 10 Ma. During this time, a more or less continuous NALB is highly probable based on fossil and geological evidence. The absence of *Corylus* in younger formations in Iceland may reflect that some parts of the NALB had experienced climates that were already too cold for the genus. All in all, the inferred divergence time appears to be too young (Tiffney 2008).

In contrast, Hoey and Parks (1991) suggested a divergence time of 16 Ma for the eastern North American-western Eurasian species pair *Liquidambar styraciflua* L. – *L. orientalis* Miller. Although not recorded in the present study, Akhmetiev et al. (1978) reported (but unfortunately did not figure) pollen of the genus from the

12 Ma Seljá locality. In view of the diverse humid warm temperate flora recorded from the 12 Ma formation, the presence of *Liquidambar* in Iceland during this time would not be in conflict with the estimated climate (Chaps. 5 and 13).

For *Rhododendron* subsection *Pontica* Milne (2004) found a divergence time of less than 4.9 Ma. Based on the assumption that the NALB had become inactive during the early half of the Cainozoic and at the latest by the early Middle Miocene (16 Ma), this author suggested that the trans-oceanic disjuncts *R. maximum* L. (eastern North America) and *R. ponticum* L. (western Eurasia) were actually connected via Beringia. Given the presence of *R.* subsection *Pontica* in Iceland from 15 to 3.7 Ma and given the climatic tolerance of the modern species (Denk 2006), such a pathway seems to be unnecessary. Also the basic assumption by Donoghue and Smith (2004) that "based on geological and palaeoclimatological evidence [...] we regard lineages with Old World-New World divergence times younger than ca. 30 Myr as unlikely to have passed through a North Atlantic land bridge, and instead more likely to have moved through Beringia" is not necessary in light of the geological and biological evidence presented above. Following the same line, Winkworth and Donoghue (2006) argued that multiple European–eastern North American disjunctions within *Viburnum* (e.g. *V. orientale* Pallas – *V. acerifolium* L.) should have involved movements during the Cainozoic from the Old World to the New World via Beringia. *Viburnum* is present in 15 and 12 Ma sediments in Iceland and during this period could freely move between North America and Europe. European-eastern North American sister relationships have also been inferred for various infrageneric groups of *Cornus* (e.g. cornelian cherries and big-bracted dogwoods; Xiang et al. 2006). In case of the big-bracted dogwoods, European representatives are extinct and known only from the fossil record. Xiang et al. (2006) inferred a multiple NALB during the Palaeogene. Scanty leaf fossils in Iceland (9–8 Ma formation) referred to as *Cornus* cannot be assigned to a particular infrageneric lineage. Nevertheless, they testify to the feasibility of the NALB for intercontinental migration during the Late Miocene.

Parks and Wendel (1990) inferred a (molecular) divergence time of 16–10 Ma for *Liriodendron*. At present, *Liriodendron* consists of two species with a disjunct distribution in eastern North America and central and southern China. Based on the assumption that the climate of Beringia would have become unsuitable for the genus by 13 Ma, these authors suggested that the disjunction between the two modern species would have been achieved prior to ca 13 Ma. The NALB was not considered as a potential factor limiting gene flow between North America and Europe because "the Atlantic had covered the North American-European connection". The presence of *Liriodendron* in 12 Ma sediments of Iceland suggests that the NALB may also have been involved in shaping the modern disjunction of the genus. For white oaks (*Quercus* infrageneric group *Quercus*), Denk and Grimm (2010) found very low levels of genetic differentiation between members of North America and Eurasia. Although these authors did not infer any divergence time based on molecular data, the genetic uniformity between intercontinental members of white oaks can partly be explained by unhindered gene flow as evidenced by the presence of

oak pollen with strong morphological affinities to white oaks in Icelandic sediments until the latest Miocene (see Chap. 9; Denk et al. 2010). In addition to the North Atlantic link, also the Bering Land Bridge may have been passable for white oaks until the latest Miocene.

Other disjunctions between Europe and eastern North America may be older (e.g. *Aesculus*, *Cercidiphyllum*; Hably et al. 2000; Grímsson et al. 2007). *Aesculus* from the 15 Ma formation in Iceland is similar to leaflets from the Early Oligocene of Spitsbergen (Schloemer-Jäger 1958). Both show morphological affinities to modern North American species, rather than the modern European *A. hippocastanum* L. At the same time, fossil taxa from the Neogene of Europe have been compared to the modern North American species *A. pavia* L. *and A. flava* Sol. *(A. velitzelosii* Knobl.; Knobloch 1998). As such, the timing and migration route of this taxon to Iceland remain unclear.

## 12.5 Conclusions

The timing of the termination of the NALB has been studied from different perspectives by specialists in different fields. Geologists have long been interested in the subsidence history of the GSTR because of its role for latitudinal heat transfer and as potential trigger of warm and cold phases during the Pleistocene (see for example, Bott et al. 1983). Palaeontologists have considered the GSTR important for the biogeographic history of marine and terrestrial organisms (Strauch 1970, 1972; Akhmetiev et al. 1978; Friedrich and Símonarson 1981; McKenna 1983a, b; Tiffney 1985, 2000, 2008; Tiffney and Manchester 2001; Denk et al. 2005, 2010; Grímsson and Denk 2005, 2007; Grímsson et al. 2007, 2008). In more recent times, biogeographers using molecular sequence data from modern organisms have become increasingly interested in the NALB and its counterpart the Bering Strait as potential corridors for plant and animal migration (e.g. Milne 2004, among many other studies).

Plant taxa requiring a mostly unbroken subaerial route were able to migrate to Iceland at the latest between 10 and 9–8 Ma from the east via the Scotland-Faeroe-Iceland route (*Fagus gussonii*) and between 7–6 and 5.5 Ma from the west via the Greenland to Iceland route (*Quercus* sp. 2). These ages are in conflict with the timing of the subsidence of the GSTR inferred from geological studies (Thiede and Eldholm 1983; Poore 2008; Table 12.1). However, recent geological studies are arriving at different dates for the subsidence of different parts of the GSTR. Poore (2008) reviewed and provided new data on the subsidence history of the GSTR and used the initiation of North Atlantic sediment drifts (all of which are well-dated) to predict the timing of overflow across various parts of the GSTR. Poore (2008) and Davies et al. (2001), among others, suggested that the Feni Drift started to be deposited in the Early Oligocene at the southeastern margin of the Faeroe to Scotland ridge, reflecting early overflow of Northern

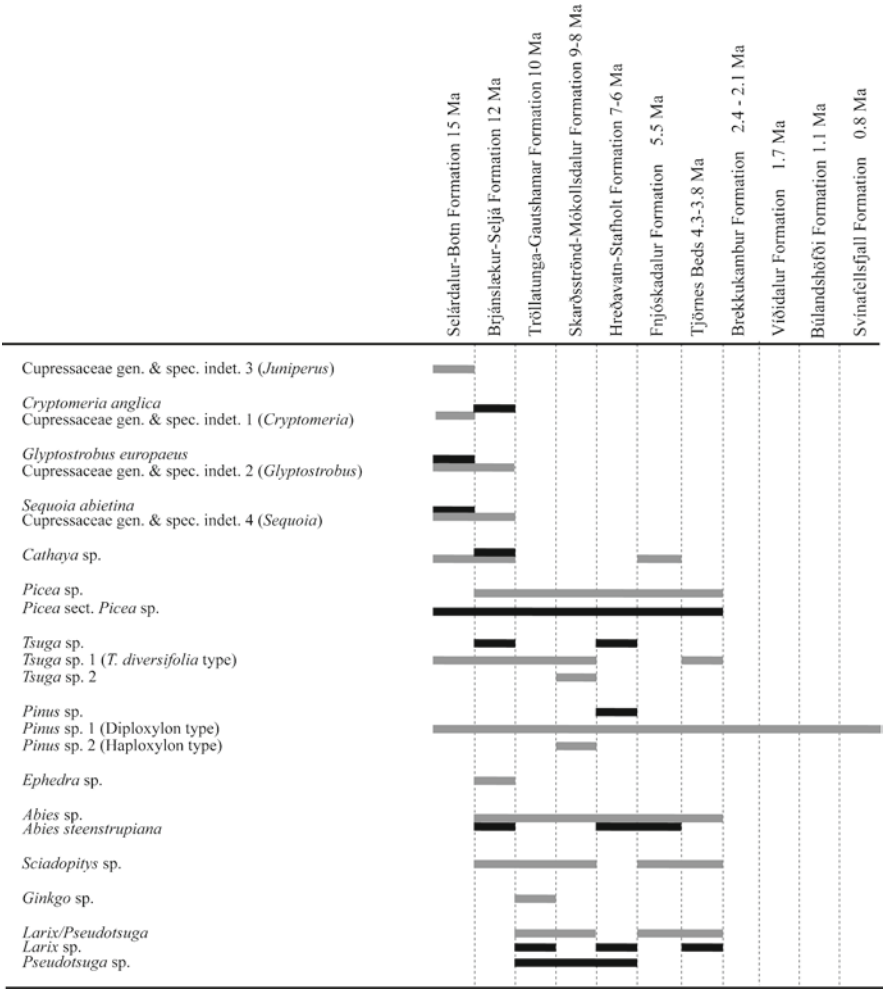
Component Water across the GSTR. This overflow would have happened via the Faeroe-Shetland Channel (see Fig. 12.1). In contrast, Stoker et al. (2005) state that "the age of formation of a deep-water connection between the basins to the north and south of the Greenland-Scotland Ridge remains unclear" (see Fig. 12.2). This uncertainty appears to be due to difficulties in determining the sources of deep water. Ramsay et al. (1998) used isotope data from benthic foraminifera to show that bottom-current circulation patterns in the Atlantic Ocean prior to the Middle Miocene were driven by southerly derived water masses. In general, geological data have yielded quite different estimates for the timing of subsidence of different parts of the GSTR (cf. Table 12.1). Divergence times for intercontinental sister taxa as inferred from phylogeographic studies are, in some cases, in accordance with evidence from the fossil record from Iceland (e.g. Milne 2004, *Rhododendron* subsect. *Pontica*). Nevertheless, other studies suggested divergence times that seem much too young (e.g. Whitcher and Wen 2001; *Corylus*). Molecular clock approaches that infer divergence times for plants have yielded conflicting dates for the same plant group depending on the method used (see Anderson 2007 for a comprehensive review and discussion of molecular clock methods). For example, Xiang et al. (1998) inferred a divergence time of 3.1 Ma for the North American and East Asian species of *Calycanthus*, whereas Zhou et al. (2006) calculated a divergence time of 6.72 ± 1.15 Ma. In general, a well documented fossil record of particular taxa is essential in order to test and complement phylogeographic studies based solely on modern taxa (Anderson 2007; see also Denk and Grimm 2009). The present study demonstrates that basic assumptions in phylogeographic studies such as the discrimination between the Bering land bridge being a corridor for plant migration before and after 30 Ma and the NALB being a corridor only before 30 Ma (e.g. Donoghue and Smith 2004) have to be revised.

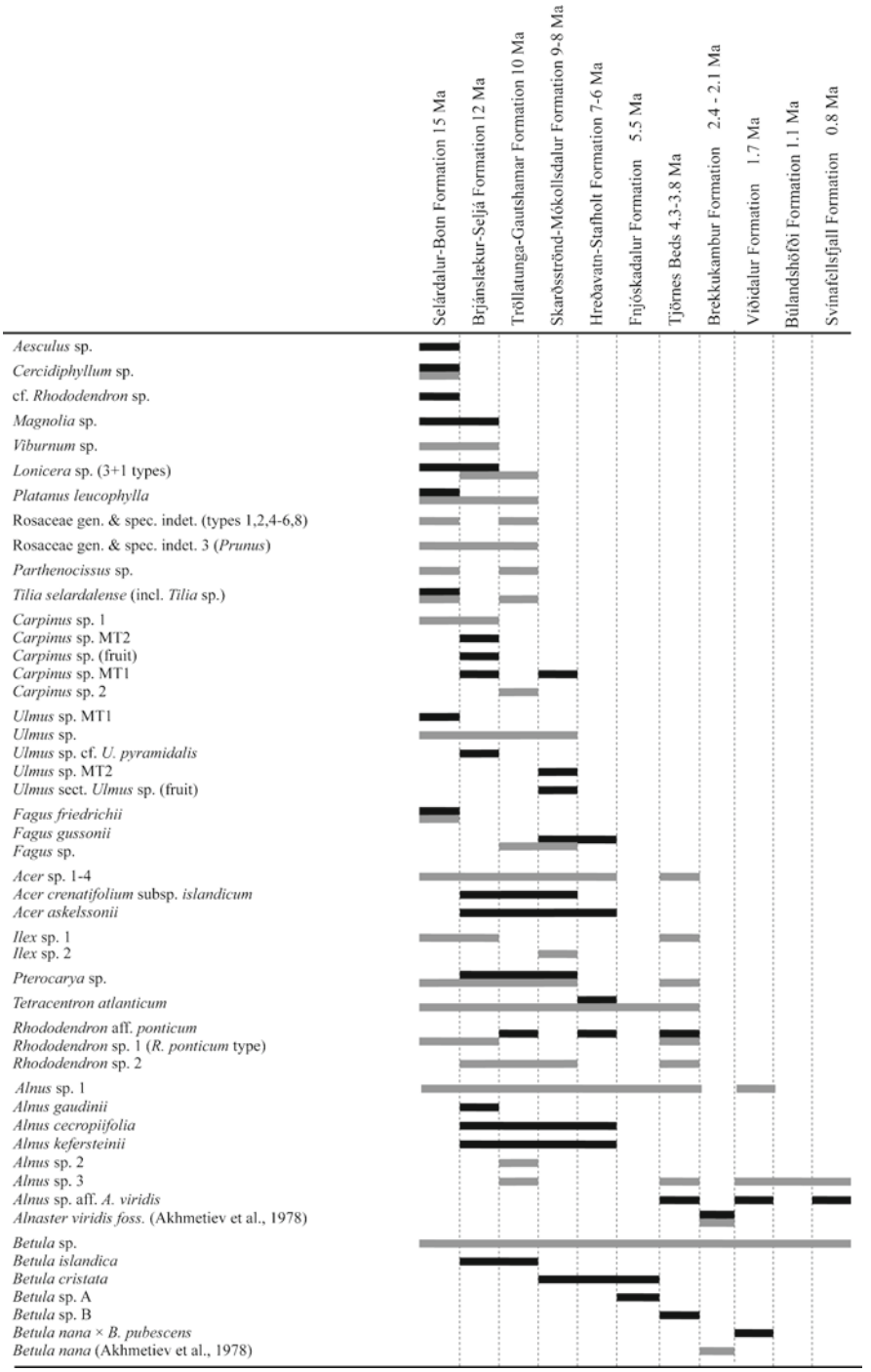
When palaeontological data are used (this study; Strauch 1972) the risk of taxonomic misidentifications cannot be avoided. Nevertheless, the taxa marking the latest plant fossil evidence for a functioning eastern and western part of the GSTR are distinctive and not likely misidentified. This appears to be direct and convincing evidence for a mostly unbroken Greenland-Scotland Transverse Ridge until 10 to 9–8 Ma, and a more or less complete Greenland-Iceland part of the GSTR until 6–5.5 Ma. A narrow Faeroe Conduit (Fig. 12.3) may not have restricted dispersal of taxa such as *Fagus*, *Quercus* or *Trigonobalanopsis*. After this time there is no plant fossil evidence for an unbroken GSTR. This may indicate the break-up of the bridge or that other factors, such as the decreasing temperature (see Chap. 13), prevented thermophilic taxa from migrating to Iceland.

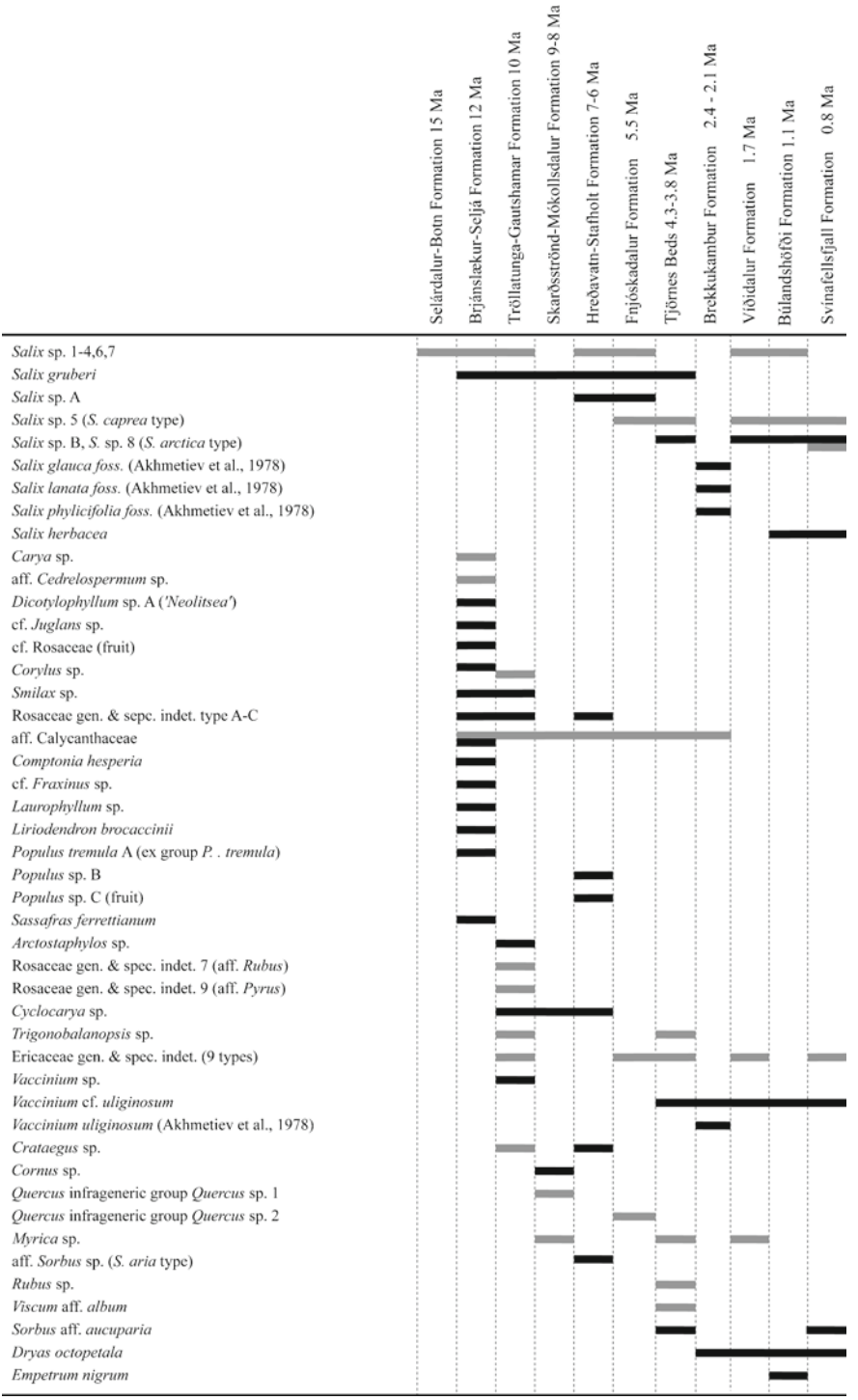
## Appendix 12.1

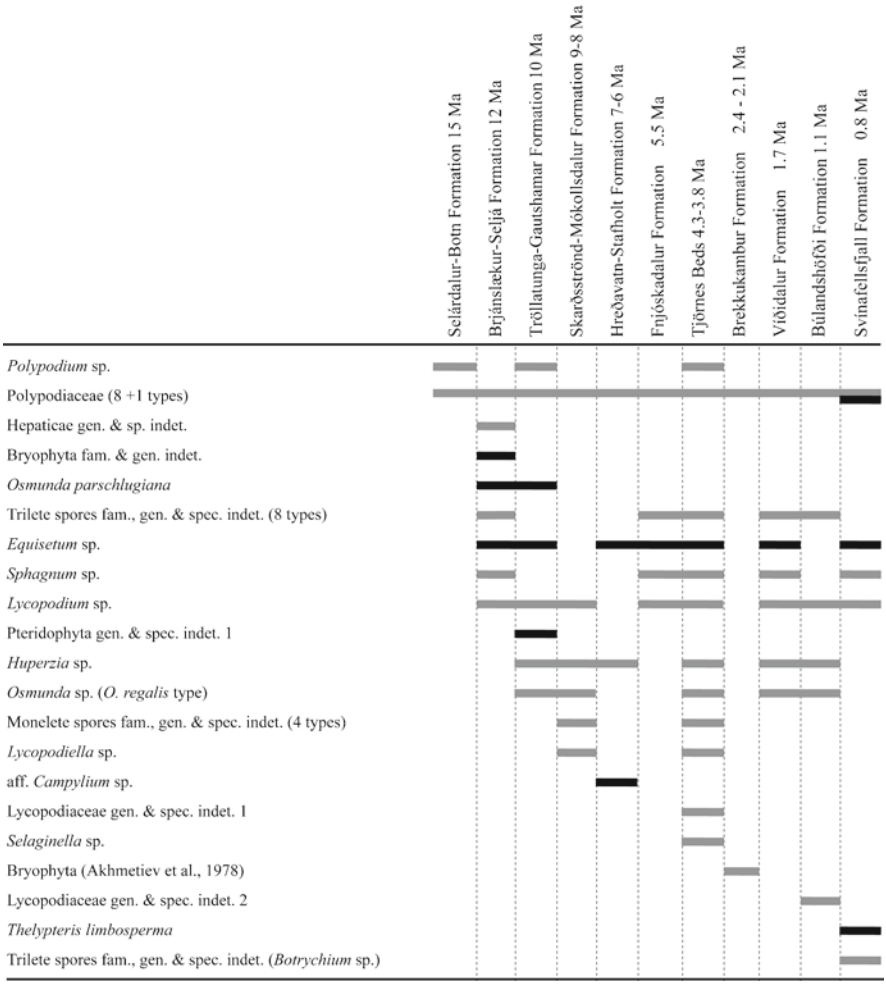
Chronological occurrence of plant (morpho-)taxa recorded from the Cainozoic of Iceland.

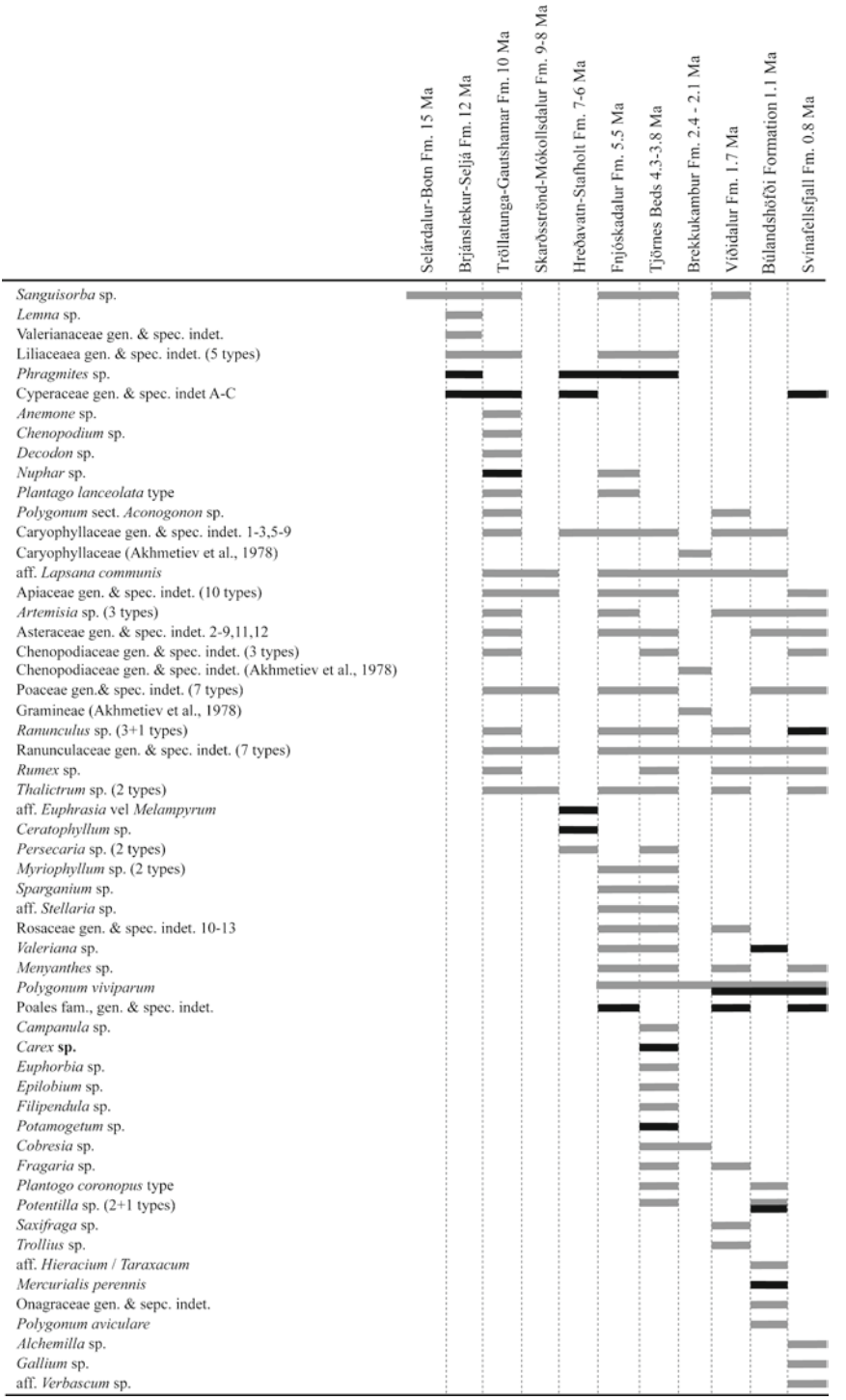
First appearances in formations younger than 15 Ma indicate that the taxon is potentially biogeographically informative (see Chaps. 4–11). Conifers, woody angiosperms, and herbaceous taxa including fern and fern allies and angiosperms, are listed separately. Grey bars indicate taxa based on pollen and spores, black bars taxa based on macro fossils.




Selárdalur-Botn Formation 15 Ma
Brjánslækur-Seljá Formation 12 Ma
Tröllatunga-Gautshamar Formation 10 Ma
Skarðsströnd-Mókollsdalur Formation 9-8 Ma
Hreðavatn-Stafholt Formation 7-6 Ma
Fnjóskadalur Formation 5.5 Ma
Tjörnes Beds 4.3-3.8 Ma
Brekkukambur Formation 2.4 - 2.1 Ma
Víðidalur Formation 1.7 Ma
Búlandshöfði Formation 1.1 Ma
Svínafellsfjall Formation 0.8 Ma
Aesculus sp.
Cercidiphyllum sp.
cf. Rhododendron sp.
Magnolia sp.
Viburnum sp.
Lonicera sp. (3+1 types)
Platanus leucophylla
Rosaceae gen. & spec. indet. (types 1,2,4-6,8)
Rosaceae gen. & spec. indet. 3 (Prunus)
Parthenocissus sp.
Tilia selardalense (incl. Tilia sp.)
Carpinus sp. 1
Carpinus sp. MT2
Carpinus sp. (fruit)
Carpinus sp. MT1
Carpinus sp. 2
Ulmus sp. MT1
Ulmus sp.
Ulmus sp. cf. U. pyramidalis
Ulmus sp. MT2
Ulmus sect. Ulmus sp. (fruit)
Fagus friedrichii
Fagus gussonii
Fagus sp.
Acer sp. 1-4
Acer crenatifolium subsp. islandicum
Acer askelssonii
Ilex sp. 1
Ilex sp. 2
Pterocarya sp.
Tetracentron atlanticum
Rhododendron aff. ponticum
Rhododendron sp. 1 (R. ponticum type)
Rhododendron sp. 2
Alnus sp. 1
Alnus gaudinii
Alnus cecropiifolia
Alnus kefersteinii
Alnus sp. 2
Alnus sp. 3
Alnus sp. aff. A. viridis
Alnaster viridis foss. (Akhmetiev et al., 1978)
Betula sp.
Betula islandica
Betula cristata
Betula sp. A
Betula sp. B
Betula nana × B. pubescens
Betula nana (Akhmetiev et al., 1978)


Selárdalur-Botn Formation 15 Ma
Brjánslækur-Selja Formation 12 Ma
Tröllatunga-Gautshamar Formation 10 Ma
Skarðsströnd-Mókollsdalur Formation 9-8 Ma
Hreðavatn-Stafholt Formation 7-6 Ma
Fnjóskadalur Formation 5.5 Ma
Tjörnes Beds 4.3-3.8 Ma
Brekkukambur Formation 2.4 - 2.1 Ma
Viðidalur Formation 1.7 Ma
Búlandshöfði Formation 1.1 Ma
Svínafellsfjall Formation 0.8 Ma
*Salix* sp. 1-4,6,7
*Salix gruberi*
*Salix* sp. A
*Salix* sp. 5 (*S. caprea* type)
*Salix* sp. B, *S.* sp. 8 (*S. arctica* type)
*Salix glauca foss.* (Akhmetiev et al., 1978)
*Salix lanata foss.* (Akhmetiev et al., 1978)
*Salix phylicifolia foss.* (Akhmetiev et al., 1978)
*Salix herbacea*
*Carya* sp.
aff. *Cedrelospermum* sp.
*Dicotylophyllum* sp. A (*'Neolitsea'*)
cf. *Juglans* sp.
cf. Rosaceae (fruit)
*Corylus* sp.
*Smilax* sp.
Rosaceae gen. & sepc. indet. type A-C
aff. Calycanthaceae
*Comptonia hesperia*
cf. *Fraxinus* sp.
*Laurophyllum* sp.
*Liriodendron brocaccinii*
*Populus tremula* A (ex group *P. . tremula*)
*Populus* sp. B
*Populus* sp. C (fruit)
*Sassafras ferrettianum*
*Arctostaphylos* sp.
Rosaceae gen. & spec. indet. 7 (aff. *Rubus*)
Rosaceae gen. & spec. indet. 9 (aff. *Pyrus*)
*Cyclocarya* sp.
*Trigonobalanopsis* sp.
Ericaceae gen. & spec. indet. (9 types)
*Vaccinium* sp.
*Vaccinium* cf. *uliginosum*
*Vaccinium uliginosum* (Akhmetiev et al., 1978)
*Crataegus* sp.
*Cornus* sp.
*Quercus* infrageneric group *Quercus* sp. 1
*Quercus* infrageneric group *Quercus* sp. 2
*Myrica* sp.
aff. *Sorbus* sp. (*S. aria* type)
*Rubus* sp.
*Viscum* aff. *album*
*Sorbus* aff. *aucuparia*
*Dryas octopetala*
*Empetrum nigrum*


Selárdalur-Botn Formation 15 Ma
Brjánslækur-Seljá Formation 12 Ma
Tröllatunga-Gautshamar Formation 10 Ma
Skarðsströnd-Mókollsdalur Formation 9-8 Ma
Hreðavatn-Stafholt Formation 7-6 Ma
Fnjóskadalur Formation 5.5 Ma
Tjörnes Beds 4.3-3.8 Ma
Brekkukambur Formation 2.4 - 2.1 Ma
Viðidalur Formation 1.7 Ma
Búlandshöfði Formation 1.1 Ma
Svínafellsfjall Formation 0.8 Ma
*Polypodium* sp.
Polypodiaceae (8 +1 types)
Hepaticae gen. & sp. indet.
Bryophyta fam. & gen. indet.
*Osmunda parschlugiana*
Trilete spores fam., gen. & spec. indet. (8 types)
*Equisetum* sp.
*Sphagnum* sp.
*Lycopodium* sp.
Pteridophyta gen. & spec. indet. 1
*Huperzia* sp.
*Osmunda* sp. (*O. regalis* type)
Monelete spores fam., gen. & spec. indet. (4 types)
*Lycopodiella* sp.
aff. *Campylium* sp.
Lycopodiaceae gen. & spec. indet. 1
*Selaginella* sp.
Bryophyta (Akhmetiev et al., 1978)
Lycopodiaceae gen. & spec. indet. 2
*Thelypteris limbosperma*
Trilete spores fam., gen. & spec. indet. (*Botrychium* sp.)


Selárdalur-Botn Fm. 15 Ma
Brjánslaekur-Seljá Fm. 12 Ma
Tröllatunga-Gautshamar Fm. 10 Ma
Skarðsströnd-Mókollsdalur Fm. 9-8 Ma
Hreðavatn-Stafholt Fm. 7-6 Ma
Fnjóskadalur Fm. 5.5 Ma
Tjörnes Beds 4.3-3.8 Ma
Brekkukambur Fm. 2.4 - 2.1 Ma
Víðidalur Fm. 1.7 Ma
Búlandshöfði Formation 1.1 Ma
Svínafellsfjall Fm. 0.8 Ma
Sanguisorba sp.
Lemna sp.
Valerianaceae gen. & spec. indet.
Liliaceaea gen. & spec. indet. (5 types)
Phragmites sp.
Cyperaceae gen. & spec. indet A-C
Anemone sp.
Chenopodium sp.
Decodon sp.
Nuphar sp.
Plantago lanceolata type
Polygonum sect. Aconogonon sp.
Caryophyllaceae gen. & spec. indet. 1-3,5-9
Caryophyllaceae (Akhmetiev et al., 1978)
aff. Lapsana communis
Apiaceae gen. & spec. indet. (10 types)
Artemisia sp. (3 types)
Asteraceae gen. & spec. indet. 2-9,11,12
Chenopodiaceae gen. & spec. indet. (3 types)
Chenopodiaceae gen. & spec. indet. (Akhmetiev et al., 1978)
Poaceae gen.& spec. indet. (7 types)
Gramineae (Akhmetiev et al., 1978)
Ranunculus sp. (3+1 types)
Ranunculaceae gen. & spec. indet. (7 types)
Rumex sp.
Thalictrum sp. (2 types)
aff. Euphrasia vel Melampyrum
Ceratophyllum sp.
Persecaria sp. (2 types)
Myriophyllum sp. (2 types)
Sparganium sp.
aff. Stellaria sp.
Rosaceae gen. & spec. indet. 10-13
Valeriana sp.
Menyanthes sp.
Polygonum viviparum
Poales fam., gen. & spec. indet.
Campanula sp.
Carex sp.
Euphorbia sp.
Epilobium sp.
Filipendula sp.
Potamogetum sp.
Cobresia sp.
Fragaria sp.
Plantogo coronopus type
Potentilla sp. (2+1 types)
Saxifraga sp.
Trollius sp.
aff. Hieracium / Taraxacum
Mercurialis perennis
Onagraceae gen. & sepc. indet.
Polygonum aviculare
Alchemilla sp.
Gallium sp.
aff. Verbascum sp.

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# Chapter 13
# Climate Evolution in the Northern North Atlantic – 15 Ma to Present

**Abstract** This chapter evaluates climatic signals from floras of 11 sedimentary rock formations from Iceland spanning the time interval 15–0.8 Ma. From 15 to 12 Ma, the climate was humid warm temperate probably with hot summers (Cfa climate) as evidenced by the presence of taxodiaceous conifers such as *Glyptostrobus* and *Cryptomeria* and warmth-loving angiosperms. The first shift towards cooler conditions occurred between ca 12 and 10 Ma; during this period the Taxodiaceae and warmth-loving angiosperms such as *Magnolia,* Lauraceae, and *Liriodendron* disappeared from the vegetation of Iceland, whereas at the same time, a massive immigration of herbaceous plants and small-leaved Ericaceae is recorded. This shift appears to reflect the transition from a Cfa to a Cfb climate. The second shift was between ca 5.5 and ca 4.4 Ma; after this interval, small-leaved *Salix* species are recorded for the first time and co-occurred with exotic elements such as the large-leaved evergreen *Rhododendron* subsection *Pontica*. Mild (Cfb climate) conditions lasted at least until ca 3.6 Ma. Between ca 3.6 and 2.4 Ma, the switch to the modern Cfc and ET climates occurred. This is reflected by the modern appearance of the Pleistocene floras. While cooling on a global scale occurred immediately after the Mid-Miocene Climatic Optimum at ca 17–15 Ma due to the rapid growth of the Eastern Antarctic Ice Sheet, mild and warm conditions lasted until at least ca 12 Ma in Iceland, underscoring the effect of warm sea currents on regional climate. The shift from a warm-house to a cold-house climate, as reflected in the floras of Iceland, coincided with the onset of large-scale glaciations in the northern hemisphere.

## 13.1 Introduction

Climate evolution is often viewed on a global scale, resulting in a mean or averaged climate signal (Pearson and Palmer 2000; Zachos et al. 2001). However, since climate is not evenly distributed across the globe, it may be helpful to

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evaluate regional or local scale signals in order to develop a more differentiated picture about the evolution of the Earth's climate and to understand how regional variants of climate interact (cf. Ramstein et al. 1997; McManus et al. 2002; Anderson and Woodhouse 2005; Robinson 2009). A good deal of our present knowledge about Neogene climates is based on data from global deep-sea isotopic records (Pearson and Palmer 2000; Zachos et al. 2001). While the climate was warm and subtropical to tropical across large parts of the northern hemisphere until the Early Eocene (ca 52 Ma; Zachos et al. 2001; Moran et al. 2006), it gradually became cooler and seasonality became more accentuated during the later parts of the Cainozoic (Ramstein et al. 1997). Studies using isotope values from marine organisms generally recognize a short and pronounced warm phase at ca 17–15 Ma, the so-called 'Mid-Miocene Climatic Optimum' (Buchardt 1978; Zachos et al. 2001) followed by a "most dramatic cooling phase" (Pearson and Palmer 2000, p. 699). Soon after the Mid-Miocene Climatic Optimum, the first ice-rafted debris are reported from the northernmost North Atlantic (14 Ma, DSDP/ODP Leg 151 site 909, Fram Strait; Thiede et al. 1998), but large-scale glaciations in the northern North Atlantic are not reported prior to ca 3 Ma (Driscoll and Haug 1998; St. John and Krissek 2002).

The northern North Atlantic has been a key area affecting global climate during the past 15 Ma due to its role in water exchange between the Arctic Ocean and the southern parts of the North Atlantic Ocean. Specifically, warm waters from the Gulf Stream-North Atlantic Current system and from the northern Sargasso Sea move to the north, forming the North Atlantic Drift Current in the Iceland Basin. The North Atlantic Drift Current is unique in that it transports warm waters to latitudes higher than in any other ocean. As the warm waters reach high North Atlantic latitudes, they give up heat and moisture to the atmosphere, cool, sink, and flow back as a cold and salty deep current, the North Atlantic Deep Water (Bischof et al. 2003; Haug et al. 2004). The initiation of the present North Atlantic current system dates back to the Middle Miocene, 16–15 Ma, at the commencing of the closure of the Central American Seaway (uplift of the Panama Sill) that blocked the exchange of tropical Atlantic and Pacific deep waters (Keller and Barron 1983; Duque-Caro 1990; Wright et al. 1991). From this time on, the developing Gulf Stream started transporting warm surface waters into the northeastern North Atlantic region (British Isles, Norway, and Iceland). Increased evaporation at high latitudes may have triggered the initial switch to a cold-house climate in the northern hemisphere, as indicated by the first ice-rafted debris pulses in the Arctic area (14 Ma; Thiede et al. 1998). At the same time, the influx of warm southerly waters ameliorated the climate in parts of the North Atlantic, and may have compensated for cooling radiating from the Arctic Ocean.

As of yet, little is known about climate development in the northern North Atlantic from the Middle Miocene onwards using terrestrial fossils, owing to the absence of sediments yielding plant and animal fossils. In this chapter, we evaluate the climatic signal from approximately 45 floras occurring in 11 plant-bearing sedimentary formations spanning the time interval 15–0.8 Ma (see Chap. 1, Table 1.2).

## 13.2 Evidence from Potential Modern Analogues of Cainozoic Plant Taxa

For all fossil taxa encountered in Icelandic Miocene to Pleistocene sediments, potential modern analogues were chosen based primarily on morphological similarity (Appendix 13.1). Depending on the taxonomic resolution (limited by the quality of the fossil record), potential modern analogues can be families, genera, or several to only a single species. For these taxa, we established their present geographic distribution including their altitudinal range using regional floras and generic monographs (e.g. Standley 1920; Meusel et al. 1965; Ohwi 1965; Hegi 1966; Browicz and Zieliński 1982, Browicz 1983; Flora of North America Editorial Committee 1993, 1997, 2010; Cao 1995; Peters 1997; Flora of China Editorial Committee 1999, 2001, 2008; Zhu and Song 1999; Iwatsuki et al. 2000, 2006; Erfmeier 2004; Luu and Thomas 2004; Sun et al. 2005). We then chose three to four climate stations that reflect the climatic extremes represented within the biogeographic distribution of each taxon and calculated the mean annual temperature (MAT).

For the present study, we used only MAT values based on the assumption that Iceland had a fully humid temperate Cf climate (Kottek et al. 2006) without severe winter frosts throughout the Neogene.

Data for climate stations were obtained from Walther and Lieth (1960, 1964) and Lieth et al. (1999), and in some cases from monographic studies of particular plant genera (Cao 1995; Erfmeier 2004). Climate stations often provide data for low altitudes. In contrast, the majority of the identified potential modern analogues display a considerable altitudinal range. To account for this, we used the moist adiabatic lapse rate, assuming that temperature changes 5°C per 1,000 altitudinal metres in humid temperate climates (Henderson-Sellers and Robinson 1986). For a number of taxa, we used Thompson et al. (1999a, 1999b, 2000, 2006) and, in few cases, the database of Utescher and Mosbrugger (2009).

We created box-plots based on the minimum MAT ($MAT_{min}$) requirements for each potential modern analogue for each sedimentary rock formation (Fig. 13.1). In addition, in Appendix 13.1, those taxa are indicated that have the four lowest minimum MAT among the taxa recovered for each sedimentary rock formation (see also Table 13.1).

The box-plots (Fig. 13.1) show the 25th and 75th percentiles (boxes), that is, the $MAT_{min}$ values below which 25% and 75% of all taxa recorded for a formation can thrive, and the 10th and 90th percentiles (whiskers). The median (horizontal lines in the boxes) divides the sample in two equally large groups, one comprising taxa with $MAT_{min}$ warmer than the median value and one comprising taxa with $MAT_{min}$ cooler than the median. For all the formations investigated, the distribution of $MAT_{min}$ is quite diffuse among the components. A clear turning point is seen first between the 12 and 10 Ma formations (compare Table 13.1) and after ca 3.6 Ma, whereas the change from ca 12 to 4.4 Ma is gradual. Warm outliers (e.g. Taxodiaceae) in the ca 15 and 12 Ma formations are outside the 5% and 95%

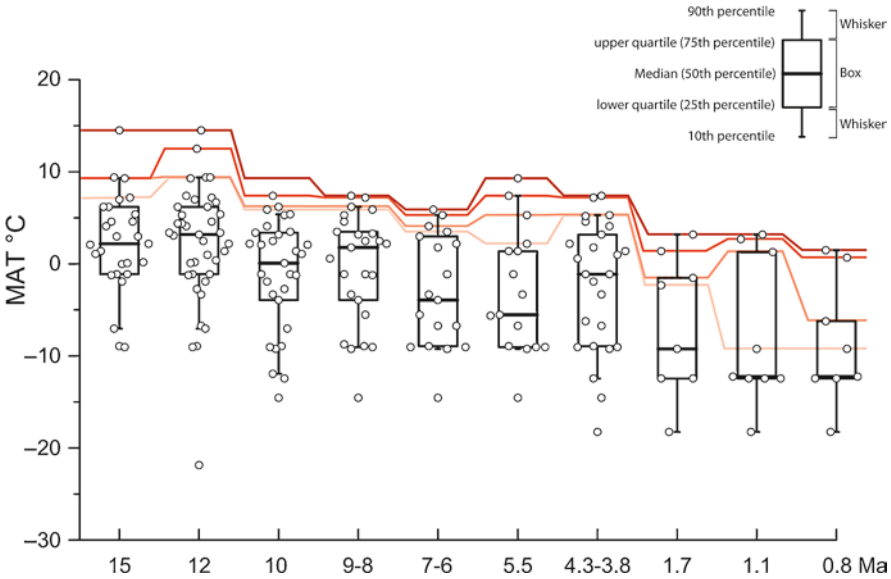



**Fig. 13.1** Box-plots based on lower limits of mean annual temperatures for potential modern analogues of fossil species recorded from Iceland (represented by *open circles*). For each formation, the *box* indicates the 25th and 75th percentiles, *whiskers* indicate the 10th and 90th percentiles, and *horizontal lines* in the boxes are medians. *Dark to light red lines* indicate the four taxa defining the four warmest $MAT_{min}$ values (i.e. the four most cold-sensitive taxa) in each formation. Note that many of these taxa are outliers in the box-plots (see also Table 13.1, Appendix 13.1)

percentiles and may have had different ecologies than their monotypic modern representatives (cf. LePage 2007).

Table 13.1 shows the range of $MAT_{min}$ defined by the four warmest values in each formation. The older formations (15 and 12 Ma) are characterized by the presence of warmth-loving Taxodiaceae, which introduce a mixed climatic signal. *Glyptostrobus* today occurs at much higher MAT than the remaining taxa recorded in the ca 15 and 12 Ma formations. However, as mentioned above, the monotypic genus *Glyptostrobus* was ecologically diversified and much more abundant during the Tertiary than at present (10–13 species in Europe; Mai 1995). The first clear climatic shift in Iceland occurred between the ca 12 and 10 Ma sedimentary rock formations but overall mild conditions persisted until at least 3.6 Ma. A second shift occurred between ca 5.5 and 4.4 Ma. During this time interval, small-leaved *Salix* appeared for the first time, introducing a double signal (Table 13.1). *Salix arctica* Pall. and *S. lanata* L. today thrive at markedly lower MAT than the remaining taxa recorded in the 4.4–3.6 Ma formation. The last shift occurred between ca 3.6 and 2.4 Ma (Fig. 13.1); this time interval marked the change towards large-scale northern hemisphere glaciations. The Pleistocene floras of Iceland (Chap. 11) were deposited during warmer interglacials, which strongly resemble modern conditions in Iceland.

**Table 13.1** Qualitative and quantitative features of late Cainozoic climates of Iceland

| | | | Estimated climate type | | Qualitative features | | | |
|---|---|---|---|---|---|---|---|---|
| **Shift (S)** | **Formation** | **$MAT_{min}$ [a] (°C)** | $MAT_{EST,\ lowlands}$ | Köppen type | Warm-loving elements | Small-leaved Ericaceae | Herbs | *Salix* |
| | 0.8 Ma | −9.2 - 1.5 | 0–5 | Cfc, ET | – | Present | Many taxa | Small-leaved |
| | 1.1 Ma | −9.2 - 3.2 | 0–5 | Cfc, ET | – | Present | Many taxa | Small-leaved |
| | 1.7 Ma | −9.2 - 3.2 | 0–5 | Cfc, ET | – | Present | Many taxa | Small-leaved |
| | 2.4–2.1[b] | – | 0–5 | Cfc, ET | – | Present | Many taxa | Small-leaved |
| S 3 | | | | | | | | |
| | 4.4–3.6 Ma | 4.1 - 7.4 | 6–8 | $Cfb_{cool\ variant}$ | Last occurrence of temperate hardwood taxa | Present | Many taxa | Small- and large-leaved |
| S 2 | | | | | | | | |
| | 5.5 Ma | 1.4 - 7.4 | 6–8 | $Cfb_{warm>cool\ variant}$ | Last occurrence of *Quercus* | Present | Many taxa | Large-leaved |
| | 7–6 Ma | 3.4 - 5.9 | 6–8 | Cfb | Last occurrence of *Fagus* | ? | Many taxa | Large-leaved |
| | 9–8 Ma | 5.9 - 7.4 | 8–10 | Cfb | *Fagus, Quercus* | ? | Many taxa | Large-leaved |
| | 10 Ma | 5.4 - 7.4 | 8–10 | Cfb | Last occurrence of *Platanus* | First appearance | First prominent invasion | Large-leaved |
| S 1 | | | | | | | | |
| | 12 Ma | 9.3 - 12.5[c] | 12–14 | Cfa | Taxodiaceae, Magnoliaceae, Lauraceae | Absent | Herbaceous elements almost absent | Large-leaved |
| | 15 Ma | 7 - 9.4[c] | 12–14 | Cfa | Taxodiaceae | Absent | Herbaceous elements almost absent | Large-leaved |

[a] Defined by the four warmest $MAT_{min}$ values (see Appendix 13.1 for a complete list of potential modern analogues)
[b] Data from Akhmetiev et al. 1978
[c] *Glyptostrobus pensilis* occurs at MAT 14.5–26.6°C

## 13.3 Evidence from Major Vegetation Changes

The ca 15 and particularly the ca 12 Ma floras contain a characteristic blend of taxa representing lowland riparian and well-drained forests and temperate upland forests. A number of warmth-loving elements are mainly confined to the floras recorded in the ca 15 and 12 Ma formations (*Glyptostrobus*, *Cercidiphyllum*, *Magnolia*, *Liriodendron*, and *Platanus*). Based on the palynological record, these floras were almost devoid of herbaceous species (see Chaps. 4, 5). Modern analogues of this ancient Icelandic vegetation can be found, for example, in riparian and foothill forests in the eastern United States, and in some montane forests along the southern and eastern coasts of the Black Sea. While the riparian vegetation encountered in the Botn flora (ca 15 Ma) contains a mixture of taxa that are at present confined to either North America (*Sequoia*) or East Asia (*Glyptostrobus*), these taxa frequently co-occurred in Tertiary plant assemblages in the northern hemisphere (e.g. Schweitzer 1974; Mai 1995; Kvaček and Rember 2000). Presently, *Glyptostrobus* thrives in almost tropical conditions in southern China (Flora of China Editorial Committee 1999). In contrast, lowland riparian forests in the eastern United States, although they do not contain *Glyptostrobus*, thrive under a Cfa climate and are closely connected to better drained lowland forests containing taxa such as *Magnolia*, *Sassafras*, *Liriodendron*, and *Fagus* (Maycock, 1994). The riparian forests of Botn (ca 15 Ma) and the better drained woods around the lake of Surtarbrandsgil (ca 12 Ma) may be fairly well comparable to the eastern North American lowland forests (Cfa climate; Appendix 13.2). The temperate uphill forests of Selárdalur (ca 15 Ma; Chap. 4) resemble various modern forests. Examples may be mixed hardwood forests of the Appalachians in eastern North America, of the coastal range south and east of the Black Sea, and of Japan (northern part of Honshu and Hokkaido; Fukarek et al. 1995). These forests are often dominated by *Fagus* species with a prominent admixture of large-leaved *Rhododendron*.

Between ca 12 and 10 Ma, several of the warmth-loving elements including the Taxodiaceae entirely disappear from the vegetation of Iceland. A novelty is the occurrence of a diverse herbaceous element in the floras of the ca 10 Ma sedimentary rock formation (Chap. 6). At the same time, a number of small-leaved Ericaceae typical of modern cool temperate areas are recorded for the first time. Overall, the changes seen in the vegetation suggest a slightly cooler climate than in the older formations (cf. Fig. 13.1). The period between ca 10 and 9–8 Ma appears to have been without major vegetational changes. Forests resembling those recorded in the two formations are typical of temperate areas (Cfb climate; Appendix 13.2) covering a rather wide range of MAT (Fig. 13.2, 2–4). A number of the taxa recorded for the ca 10 and 9–8 Ma formations are at present restricted to relict areas resulting from disruptions of formerly larger and continuous areas during the Tertiary (e.g. *Calycanthaceae*, Mai 1995; *Rhododendron* sect. *Pontica*, Milne 2004; *Pterocarya fraxinifolia* (Lam.) Spach, e.g. Mai 1995). Although their present range is geographically restricted, they tolerate a wide range of climates (Cfa, Cfb warm to cool variants, Fig. 13.2; cf. Denk 2006). The

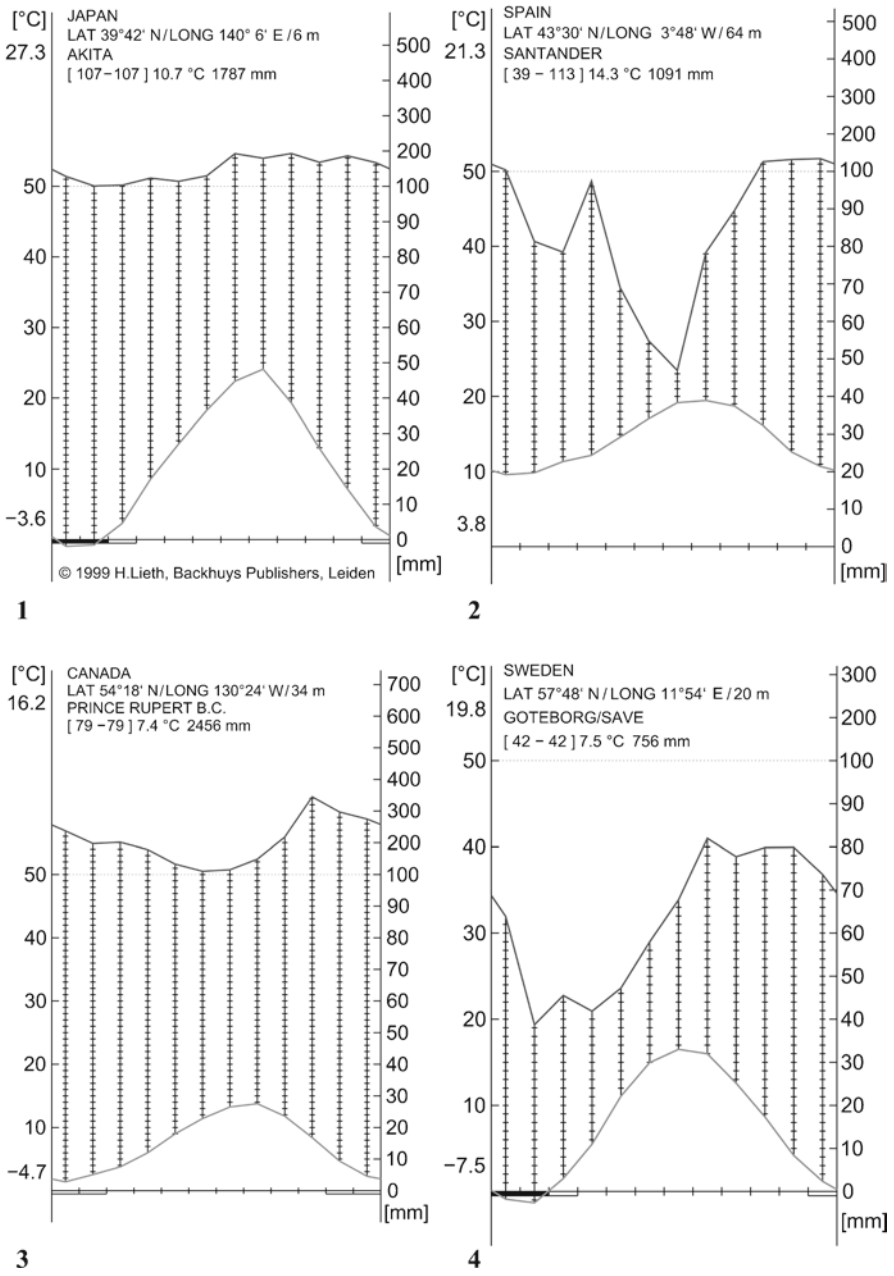



**Fig. 13.2** Representative climate stations for Cfa and Cfb climates (Climate diagrams from Lieth et al. 1999). **1**. Akita, Cfa climate. **2**. Santander, Cfb climate. **3**. Prince Rupert, Cfb climate. **4**. Gothenburg, Cfb climate (climate types according to Köppen, cf. Kottek et al. 2006)

gradual cooling during the Late Miocene is probably reflected by the decline of *Fagus* between 8 and 5.5 Ma. While a dominant element in the 9–8 Ma formation, only a single leaf and nut likely belonging to the genus, are recorded in the 7–6 Ma formation, and the genus is absent from the ca 5.5 Ma and younger formations. The subtle shift recorded in the vegetation may correspond to a change from warm to cool variants of a Cfb climate (see climate diagrams for Prince Rupert and Gothenburg in Fig. 13.2, 3 and 4).

The last phase of prevailing mild conditions is recorded in the Tjörnes floras (4.4–3.6 Ma; Chap. 10; Fig. 13.1). Humid mild conditions are reflected by the presence of evergreen (understorey) taxa, such as *Rhododendron* aff. *ponticum*, *Ilex*, and, surprisingly, *Trigonobalanopsis*, representing an extinct type of Fagaceae. Mixed broadleaved deciduous and conifer forests were made up of *Acer*, *Pterocarya*, *Alnus cecropiifolia* (Ettingsh). Berger with an admixture of *Abies* and other conifers. Between ca 3.6 (beginning of the Late Pliocene) and 2.4 Ma (Early Pleistocene), the switch from mild and warm conditions to the present cool to cold climate occurred. This is mainly marked by the absence of large-leaved *Salix* in the 2.4–0.8 Ma floras and the dominance of small-leaved *Salix* spp., *Betula pubescens* Ehrh. and *B. nana* L. leaf types, Arctic-Alpine Ericaceae, and *Sorbus aucuparia* (Chaix.) DC. All these elements are also found in the modern vegetation of Iceland. One exception among the woody taxa recorded in the 2.4–0.8 Ma floras is *Alnus viridis*, which is absent from the present flora of Iceland but is common in Greenland.

## 13.4 Estimated Climate Types for the Sedimentary Formations 15–0.8 Ma

Climatic conditions during the time of deposition of the 15–0.8 Ma sedimentary rock formations in Iceland can be estimated from temperature requirements of potential modern analogues (Appendix 13.1) and from modern vegetation types comparable to the ancient ones (see above). Overall, a Cfa climate can be inferred for lowland areas at the time when the ca 15 and 12 Ma formations were deposited, that is, a humid subtropical mild climate with no dry season and a relatively hot summer (Table 13.2; Appendix 13.2). The presence of various Taxodiaceae and *Fagus* suggests a lowland-upland vegetation corresponding to modern forests in the (south)eastern United States, the southern and eastern coasts of the Black Sea, and (south)eastern China and Japan (except Hokkaido). A Cf, i.e. fully humid, climate type is highly likely given the position of Iceland in the centre of the northern North Atlantic; a Cfa climate, indicating relatively hot summers, is inferred from the presence of *Glyptostrobus*, *Laurophyllum, Platanus*, and *Liriodendron*, among others. It should be noted that a Cfa climate does not necessarily differ from a Cfb climate in terms of MAT, but mainly in the temperature of the four warmest months (see Fig. 13.2, 1 and 2; Akita versus Santander). Climates comparable to the one estimated for the 15 and 12 Ma formations are found,

**Table 13.2** Climatic parameters of Köppen climate types relevant for late Cainozoic floras of Iceland (From Kottek et al. 2006; see also Appendix 13.2)

| **Köppen climate types** | | |
|---|---|---|
| **C .....** | Warm temperate; T coldest month ≥ −3.0°C and <18°C | |
| **D .....** | Snow climate; T coldest month < −3.0°C | |
| **f ...** | Fully humid without dry season | |
| **w ...** | Winter dry | |
| **s ...** | Summer dry ($P_{Smin} < P_{Wmin}$; $P_{Wmax} > 3P_{Smin}$; $P_{Smin} < 40$ mm) | |
| **a** | Hot summer; T warmest month ≥22°C | **Cfa** |
| **b** | Warm summer; T warmest month <22°C and ≥4 months >10°C | **Cfb** |
| **c** | Cool summer; T warmest month <22°C and <4 months >10°C and coldest month > −38°C | **Cfc** |
| **E .....** | Polar; T warmest month <10°C | |
| **T ...** | Tundra; T warmest month >0°C | **ET** |

$P_{Smin/max}$ = minimum/maximum summer precipitation
$P_{Wmin/max}$ = minimum/maximum winter precipitation

for example, in Akita (Fig. 13.2), northern Honshu, and Wajima (see Fig. 4.3), central eastern Honshu.

Cfb climates were most likely present in upland areas during time of sedimentation of the ca 15 and 12 sedimentary rock formations and from ca 10 to 3.6 Ma. Summer temperatures in a Cfb climate basically are cooler than in a Cfa climate (Table 13.2). Cfb climates are typical of the temperate parts of Europe, including most of the British Isles. This climate type includes a wide range of mean annual temperatures as can be seen in Fig. 13.2 (compare Gothenburg with Santander). In southwestern Europe, Asia Minor (along the southern and eastern coast of the Black Sea), and Japan, Cfa climates gradually change into Cfb climates. In North America, Cfb climates are much less common than Cfa climates and are restricted to northwestern North America and higher elevations in the Appalachian Mountains (Kottek et al. 2006).

From ca 3 Ma onwards, a Cfc climate, similar to the Cfb type but with cool summers, prevailed during the warm phases. Also, ET climate types (Tundra climate with no true summer) occurred from that time on (Table 13.2; Appendix 13.2). Today, the southern and southwestern coasts of Iceland, including the area of Svínafell (0.8 Ma sedimentary rock formation; Chap. 11) and some interior fjords and valleys in the east and north have a Cfc climate, whereas the remaining island has an ET climate (Sjörs 2004; Kottek et al. 2006).

## 13.5 Climate Evolution in the Northern North Atlantic

The Earth's climate has gradually cooled during the Tertiary (the last 65 Ma). This trend has been punctuated by three steps marked by higher rates of cooling; during the Late Eocene-Early Oligocene (ca 34 Ma), during the Middle Miocene (ca 14 Ma), and at the Pliocene-Pleistocene boundary (ca 2.6 Ma; Zachos et al. 2001;

Gibbard and Cohen 2009). The first two steps were mainly triggered by two phases of rapid expansion of the Antarctic continental ice sheets, whereas the third one was a consequence of the onset of major ice sheets in the northern hemisphere.

### *13.5.1 Mid-Miocene Climatic Optimum*

Global climate change for this period is mostly reconstructed from the deep-sea stable isotope record (Zachos et al. 2001; Zhao et al. 2001; Holbourn et al. 2005; among many others). A phase of global warming, the Mid-Miocene Climatic Optimum, peaked between ca 17 and 15 Ma and was followed by cooling and re-establishment of a major ice sheet on Antarctica (Zachos et al. 2001). The termination of the Miocene warm phase is marked by the Middle Miocene climatic transition between ca 14.2 and 13.8 Ma. Stepwise cooling of Antarctic Circumpolar surface waters (Shevenell et al. 2004) was followed by a rapid expansion of the Antarctic ice sheet between 13.9 and 13.8 Ma (Holbourn et al. 2005).

A number of studies using palaeontological data from terrestrial sediments of both hemispheres detected a similar signal of marked warming followed by rapid cooling in the mid-Miocene. White et al. (1997) found abundant thermophilous broadleaved deciduous and conifer taxa in 15 Ma sediments from northwestern Canada and Alaska (Fagaceae, Taxodiaceae, Juglandaceae), which are entirely absent in younger sediments that are dominated by Betulaceae and Pinaceae, and from 7 Ma onwards, by herbaceous taxa. Floras clearly indicating warm conditions (Cfa climate) are also recorded by Matthews and Ovenden (1990) from 18 Ma sediments of Banks Island, N.W.T. For Central Europe, Kvaček et al. (2006) inferred a clear cooling trend from the Karpatian-early Badenian (corresponding to the Mid-Miocene Climatic Optimum) to the late Badenian-earliest Sarmatian (ca 12.6 Ma), which is fairly consistent with the oxygen isotope curve. From East Antarctica, Lewis et al. (2009) report the extinction of tundra plants and animals between ca 14 and 13.8 Ma, caused by rapidly expanding glaciers during this time interval. They suggest that the transition to cold-based, alpine glacial regimes at 13.85 Ma was never subsequently reversed.

In stark contrast, deteriorating conditions between 15 and 12 Ma as recorded in continental floras and by marine isotope data can not be seen in the climatic signal of well-dated late Cainozoic floras of Iceland. Why is this?

The Middle Miocene was a period of tectonic changes that had dramatic consequences on global ocean circulation, which, in turn, were important factors for Cainozoic climatic development. Tectonically, the uplift of the Panama Sill blocked the exchange of deep water between the Atlantic and Pacific Oceans (Keller and Barron 1983) and the collision of the African and Eurasian plates caused the termination of the connection between the Atlantic and the Indian Oceans. Thus, a deep-water source in the northern Indian Ocean (Tethyan Indian Saline Water) was terminated at about 15 Ma (Woodruff and Savin 1989; Flower and Kennett 1995). The Indian-Paratethys-Caribbean Seaway was replaced by north–south currents in

the northern and southern Atlantic. As a consequence, diminished heat transport to the high southern latitudes and an increase in the (cold) Southern Component Water fostered major Eastern Antarctic Ice Sheet growth, leading to global cooling (Flower and Kennett 1995). At the same time, the re-organisation of the global ocean currents led to an intensifying Gulf Stream transporting warm surface water into the northeastern North Atlantic region (Keller and Barron 1983). Increased evaporation at high latitudes triggered the switch to a cold-house climate in the northern hemisphere, as indicated by the first ice-rafted debris pulses in the High Arctic (14 Ma; Thiede and Myhre 1995; Thiede et al. 1998).

Mild and warm conditions in Iceland outlasted the Mid-Miocene Climatic Optimum by at least 2 million years (Fig. 13.1, Table 13.1). This could have been caused by the influx of warm southerly waters (the Gulf Stream), which ameliorated the climate in the central parts of the northern North Atlantic (Iceland), and may have compensated for cooling radiating from the Arctic Ocean.

Interestingly, a similar scenario has been reported for the last interglacial warm period. McManus et al. (2002) found that regional warm conditions in the northern North Atlantic were considerably prolonged relative to the duration of the marine isotope stage MIS 5e (reflecting a minimum in global ice volume) and continued well into the glacial growth of MIS 5d. They concluded that enhanced thermohaline circulation provided the heat transport that helped prolong the interglacial warmth, while at the same time provided an ideal moisture source for ice-sheet growth. This demonstrates the direct influence of the thermohaline circulation and the warm Gulf Stream on the regional climate. Comparable conditions may have been present in southern New Zealand. Field et al. (2009) found no significant change in the palynological content of an inshore marine sequence spanning the time interval from ca 16 to ca 11.6 Ma, although a clear positive $\delta^{18}O$ baseline shift was detected between 13.9 and 13.8 Ma. These authors speculated that the mid-latitude maritime setting muted the effects of Middle Miocene global climate change.

### *13.5.2 Late Miocene Gradual Cooling*

The sudden appearance of many herbaceous plants recorded in the ca 10 Ma floras, and the presence of small-leaved Ericaceae, are indicative of climate cooling in the early Late Miocene (Chap. 6). Herbaceous taxa such as Asteraceae, Caryophyllaceae, Chenopodiaceae, and some Ranunculaceae (*Thalictrum*) and Rosaceae (*Potentilla*) became important elements of the European vegetation in the course of the Miocene (Mai 1995), indicating the availability of more open landscapes, which, in turn, may have been the result of cooler and/or more continental conditions (Ramstein et al. 1997). Mild conditions prevailed until at least 9–8 Ma (abundant *Fagus*; Chap. 7).

Several ice-rafted debris pulses in the Fram Strait recorded at the DSDP/ODP Leg 151 site 909 between 10.8 and 8.6 Ma, around 7.2, 6.8, and 6.3 Ma indicate a further stepwise increase of northern hemisphere cooling (Thiede et al. 1998).

Larsen et al. (1994) suggested that cooling in southeastern Greenland started after 10 Ma and glaciers large enough to reach sea level were present at around 7 Ma, contemporaneous with southern hemisphere glacial expansion. Gradual cooling is also recorded in the oxygen isotope curve (Abreu and Haddad 1998) for the Late Miocene.

### *13.5.3 Pliocene Warming and Onset of Northern Hemisphere Glaciations*

The final closure of the Central American Seaway between 5 and 3.6 Ma partitioned the Atlantic and Pacific oceans and dramatically changed global ocean circulation. Increased evaporation in the tropical Atlantic increased the salinity of the Atlantic. At the same time, the Gulf Stream intensified and transported more salty and warm water masses to high latitudes where they cooled and sank, fuelling the Global Ocean Conveyor (Haug et al. 2004). The warm and steady climate that the Earth experienced between 4.5 and 2.7 Ma, and that was to a large degree a consequence of this re-arrangement of ocean currents, has been termed the Mid-Pliocene Climatic Optimum (Dowsett et al. 1996, 2009; Raymo et al. 1996; Kim and Crowley 2000; Robinson 2009). Raymo et al. (1996) suggested that this warm period was associated with increased North Atlantic Deep Water production and that a stronger thermohaline circulation in the Atlantic Ocean may have enhanced sea ice retreat and decreasing high latitude albedo.

In Iceland, terrestrial sediments yielding the warm Pliocene floras of Tjörnes (4.4–3.6 Ma) are intercalated within the marine Tjörnes beds. The floras of Tjörnes contain a number of warmth-loving exotic taxa (see Sect. 13.3). Based on the oxygen isotope composition of marine molluscs spanning a sequence from 4.3 to 2.6 Ma, Buchardt and Símonarson (2003) reconstructed warm-water conditions (summer temperatures between 10 and 15°C) interrupted by a few cold spells of which the most prominent coincided with the first major glaciation in southeastern Greenland at ca 3.5 Ma ( St. John and Krissek 2002). Warmth-loving plant taxa are also present in 4–3 Ma sediments from the Canadian Arctic Archipelago (Meighen Island, Ellesmere Island; Matthews and Ovenden 1990) and Alaska (Matthews et al. 2003). Together with an unusual warm insect fauna (Elias and Matthews 2002) and an exceptionally rich mammal fauna (Ellesmere Island; Tedford and Harrington 2003), these data provide strong evidence for markedly warmer conditions than today in Arctic regions of the northern hemisphere just before the onset of widespread northern hemisphere glacial expansion at ca 2.7 Ma.

At 2.55–2.45 Ma, the first extensive glaciation occurred in Iceland (Eiríksson 2008) coinciding with the first occurrence of high-Arctic shallow marine molluscs such as *Portlandia arctica* (Gray) (Símonarson and Leifsdóttir 2002). The youngest floras described in this book were deposited in Pleistocene interglacial sediments (2.4–2.1, Hvalfjördur, Akhmetiev et al. 1978; 1.7–0.8 Ma floras, Chap. 11).

# Appendix 13.1

Taxa lists for 10 formations from the Cainozoic of Iceland indicating potential modern analogues and their climatic (MAT) parameters

| Selárdalur-Botn Formation TAXA | Potential modern analogue | MAT low °C | MAT high °C | | | |
|---|---|---|---|---|---|---|
| Polypodiaceae | | | | | | |
| *Polypodium* sp. 1 | *Polypodium* | Cosmopolitan | | | | |
| Polypodiaceae gen. et spec. indet. 1 | Polypodiaceae | Cosmopolitan | | | | |
| Cupressaceae s.l | | | | | | |
| *Cryptomeria* sp. | *Cryptomeria japonica* | 7[a] | 20.5 | | | |
| *Glyptostrobus europaeus* | *Glyptostrobus pensilis* | 14.5 | 26.6 | | | |
| *Juniperus* sp. | *Juniperus* | Cosmopolitan | | | | |
| *Sequoia abietina* | *Sequoia sempervirens* | 9.4 | 15.3 | | | |
| Pinaceae | | | | | | |
| *Cathaya* sp. | *Cathaya argyrophylla* | 9.3 | 18.6 | | | |
| *?Picea* sp | *Picea* | –8.9 | 21.7 | | | |
| *Pinus* sp. 1 Diploxylon | *Pinus* | Cosmopolitan | | | | |
| *Tsuga* sp. 1 | *Tsuga diversifolia* | 6.2 | 17.2 | | | |
| Aquifoliaceae | | | | | | |
| *Ilex* sp. 1 | *Ilex aquifolium* | 7.2 | 18.2 | | | |
| | *Ilex opaca* | 7.4 | 22.4 | | 7.2 | 22.4 |
| | *Ilex decidua* | 11.1 | 22.1 | | | |
| Betulaceae | | | | | | |
| *Alnus* sp. 1 | *Alnus japonica* | 0.2 | 24.4 | | | |
| | *Alnus rhombifolia* | 0 | 16.3 | | 0 | 24.5 |
| | *Alnus subcordata* | 7.2 | 18.6 | | | |

(continued)

Taxa lists for 10 formations from the Cainozoic of Iceland indicating potential modern analogues and their climatic (MAT) parameters (continued)

| Selárdalur-Botn Formation TAXA | Potential modern analogue | MAT low °C | MAT high °C | | |
|---|---|---|---|---|---|
| *Betula* sp. 1 | *Betula ermannii* | –7 | 14.6 | | |
| | *Betula delavayi* | 4.1 | 15.3 | | |
| | *Betula chinensis* var. *fargesii* | 2.9 | 11.4 | –7 | 22.5 |
| | *Betula utilis* | –0.4 | 22.5 | | |
| *Carpinus* sp. | *Carpinus cordata* | 3 | 16.7 | | |
| Caprifoliaceae | | | | | |
| *Lonicera* sp. | *Lonicera xylosteum* | 0.1 | 14.9 | | |
| *Viburnum* sp. | | | | | |
| Cercidiphyllaceae | | | | | |
| *Cercidiphyllum* sp. | *Cercidiphyllum japonicum* | 7.6 | 17 | | |
| | *Cercidiphyllum magnificum* | 4.6 | 11.6 | 4.6 | 17 |
| Ericaceae | | | | | |
| cf. *Rhododendron* sp. | *Rhododendron maximum* | 4.6 | 17.5 | | |
| *Rhododendron* sp. 1 | *Rhododendron ponticum* | 4.1 | 18.3 | | |
| Fagaceae | | | | | |
| *Fagus friedrichii* | *Fagus crenata* | 3 | 13 | 3 | 22.1 |
| | *Fagus grandifolia* | 4.4 | 22.1 | | |
| Juglandaceae | | | | | |
| *Pterocarya* sp. | *Pterocarya macrocarpa* | –1.9 | 19.8 | | |
| Liliaceae | | | | | |
| Liliaceae gen. et spec. indet. 1 | Liliaceae | Cosmopolitan | | | |
| Magnoliaceae | | | | | |
| cf. *Magnolia* sp. | *Magnolia* | 6.2 | 27 | | |
| Platanaceae | | | | | |
| *Platanus leucophylla* | *Platanus occidentalis* | 5.4 | 21.1 | | |

| | | | | | | |
|---|---|---|---|---|---|---|
| Rosaceae gen et. spec. indet. 1 | Rosaceae | Cosmopolitan | | | | |
| Rosaceae gen et. spec. indet. 2 | Rosaceae | Cosmopolitan | | | | |
| Rosaceae gen et. spec. indet. 3 | Rosaceae | Cosmopolitan | | | | |
| *Sanguisorba* sp. | *Sanguisorba officinalis* | 1.4 | 15.8 | | | |
| Salicaceae | | | | | | |
| *Salix* sp. 1 | *Salix caprea* | –9 | 17.8 | } | –9 | 23.2 |
| | *Salix scouleriana* | –5.6 | 23.2 | | | |
| Sapindaceae | | | | | | |
| *Acer* sp. 1 | *Acer rubrum* | –1.1 | 23.8 | | | |
| *Acer* sp. 2 | *Acer saccharum* | –1.1 | 15.8 | | | |
| *Aesculus* sp. | *Aesculus flava* | 8.6 | 22.1 | } | 0.2 | 24.4 |
| | *Aesculus pavia* | 0.2 | 24.4 | | | |
| Tiliaceae | | | | | | |
| *Tilia selardalense* | *Tilia americana* | 1.1 | 16.1 | } | 1.1 | 16.1 |
| | *Tilia platyphyllos* | 3.4 | 14 | | | |
| Trochodendraceae | | | | | | |
| *Tetracentron atlanticum* | *Tetracentron sinense* | 2.2 | 19 | | | |
| Ulmaceae | | | | | | |
| *Ulmus* sp. MTI | *Ulmus* | –1.2 | 24.3 | | | |
| Vitaceae | | | | | | |
| *Parthenocissus* sp. | *Parthenocissus quinquefolia* | 2.1 | 19.8 | } | 2.1 | 21.4 |
| | *Parthenocissus laetevirens* | 9.3 | 21.4 | | | |
| Incertae sedis – Magnoliophyta | | | | | | |
| Pollen type 1 | – | – | – | | | |

[a] Grey shading indicates the four warmest $MAT_{min}$ values encountered; dark grey shading indicates this taxon is a climatic outlier (see text for explanation)

Taxa lists for 10 formations from the Cainozoic of Iceland indicating potential modern analogues and their climatic (MAT) parameters (continued)

| Brjánslækur-Seljá Formation TAXA | Potential modern analogue | MAT low °C | MAT high °C |
|---|---|---|---|
| Bryophyta | | | |
| Hepaticae gen. et spec. indet. | Hepaticae | Cosmopolitan | |
| Lycopodiaceae | | | |
| *Lycopodium* sp. | *Lycopodium* | Cosmopolitan | |
| Equisetaceae | | | |
| *Equisetum* sp. | *Equisetum* | Cosmopolitan | |
| Osmundaceae | | | |
| *Osmunda parschlugiana* | *Osmunda regalis* | 3.2 | 23.9 |
| Polypodiaceae | | | |
| Polypodiaceae gen. et spec. indet. 1 | Polypodiaceae | Cosmopolitan | |
| Polypodiaceae gen. et spec. indet. 2 | Polypodiaceae | Cosmopolitan | |
| Incertae sedis - unassigned spores | | | |
| Trilete spore fam. gen. et spec. indet. 1 | – | – | |
| Ephedraceae | | | |
| *Ephedra* sp. | *Ephedra distachya* | 9.4 | 18.9 |
| Cupressaceae incl. Taxodiaceae | | | |
| *Cryptomeria anglica* | *Cryptomeria japonica* | 7 | 20.5 |
| *Glyptostrobus* sp. | *Glyptostrobus pensilis* | 14.5 | 26.6 |
| *Sequoia* sp. | *Sequoia sempervirens* | 9.4 | 15.3 |
| Pinaceae | | | |
| *Abies steenstrupiana* | *Abies* | –6.7 | 27.4 |
| *Cathaya* sp. | *Cathaya argyrophylla* | 9.3 | 18.6 |
| *Picea* sect. *Picea* | *Picea* | –8.9 | 21.7 |
| *Tsuga* sp. | *Tsuga diversifolia* | 6.2 | 17.2 |
| Sciadopityaceae | | | |
| *Sciadopitys* sp. | *Sciadopitys verticillata* | 7.4 | 16.6 |
| Aquifoliaceae | | | |

| | | | | | |
|---|---|---|---|---|---|
| *Ilex* sp. 1 | *Ilex aquifolium* | 7.2 | 18.2 | 7.2 | 22.4 |
| | *Ilex opaca* | 7.4 | 22.4 | | |
| | *Ilex decidua* | 11.1 | 21.1 | | |
| Betulaceae | | | | | |
| *Alnus cecropiifolia* | *Alnus glutinosa* | –3.3 | 17.4 | –3.3 | 22.4 |
| | *Alnus nitida* | 5.6 | 22.4 | | |
| | *Alnus rhombifolia* | 0 | 16.3 | | |
| *Alnus gaudinii* | *Alnus japonica* | 0.2 | 24.4 | 0.2 | 24.4 |
| | *Alnus subcordata* | 7.2 | 18.6 | | |
| *Betula islandica* | *Betula ermannii* | –7 | 14.6 | –7 | 22.5 |
| | *Betula delavayi* | 4.1 | 15.3 | | |
| | *Betula utilis* | –0.4 | 22.5 | | |
| *Carpinus* sp. MT1 | *Carpinus betulus* | 4.3 | 15.5 | 2.5 | 28.2 |
| | *Carpinus caroliniana* | 2.5 | 28.2 | | |
| *Carpinus* sp. MT2 | *Carpinus cordata* | 3 | 16.7 | | |
| *Corylus* sp. | *Corylus americana* | –0.4 | 17.9 | –2.7 | 19 |
| | *Corylus avellana* | 1.3 | 19 | | |
| | *Corylus chinensis* | –2.7 | 18.4 | | |
| Calycanthaceae | | | | | |
| aff. Calycanthaceae | *Calycanthus chinensis* | 11.5 | 13.4 | 5.3 | 20 |
| | *Calycanthus floridus* | 8.7 | 19.4 | | |
| | *Calycanthus occidentalis* | 5.3 | 18.3 | | |
| | *Chimonanthus* spp. | 7 | 20 | | |
| Caprifoliaceae | | | | | |
| *Lonicera* sp. 1 | *Lonicera xylosteum* | 0.1 | 14.9 | | |
| *Viburnum* sp. | *Viburnum opulus* | 1 | 14 | | |
| Cyperaceae | | | | | |
| Cyperaceae gen. et spec. indet. A | Cyperaceae | Cosmopolitan | | | |
| Ericaceae | | | | | |
| *Rhododendron* sp. 1 | *Rhododendron ponticum* | 4.1 | 18.3 | | |
| R*hododendron* sp. 2 | *Rhododendron maximum* | 4.6 | 17.5 | | |

(continued)

Taxa lists for 10 formations from the Cainozoic of Iceland indicating potential modern analogues and their climatic (MAT) parameters (continued)

| Brjánslækur-Seljá Formation TAXA | Potential modern analogue | MAT low °C | MAT high °C | | |
|---|---|---|---|---|---|
| Juglandaceae | | | | | |
| *Carya* sp. | *Carya cathayensis* | 8.5 | 18.4 | 4.4 | 22.4 |
| | *Carya glabra* | 4.4 | 22.4 | | |
| cf. *Juglans* | *Juglans mandshurica* | 0.4 | 20 | | |
| *Pterocarya* sp. | *Pterocarya fraxinifolia* | 8.1 | 18.1 | –1.9 | 19.1 |
| | *Pterocarya macrocarpa* | –1.9 | 19.1 | | |
| Lauraceae | | | | | |
| *Laurophyllum* sp. (*Laurus*) | *Laurus nobilis* | 12.5 | 19.2 | | |
| *Sassafras ferrettianum* | *Sassafras albidum* | 6.7 | 18.1 | 6.7 | 20.6 |
| | *Sassafras tzumu* | 8.4 | 19.1 | | |
| Lemnaceae | | | | | |
| *Lemna* sp. | *Lemna* | Cosmopolitan | | | |
| Magnoliaceae | | | | | |
| *Liriodendron procaccinii* | *Liriodendron tulipifera* | 4.4 | 22 | 4.4 | 22 |
| | *Liriodendron chinensis* | 11 | | | |
| *Magnolia* sp. | *Magnolia* | 6.2 | 18<br>27 | | |
| Myricaceae | | | | | |
| *Comptonia hesperia* | *Comptonia peregrina* | 3.4 | 15.6 | | |
| Oleaceae | | | | | |
| cf. *Fraxinus* sp. | *Fraxinus* | 3.1 | 21.1 | | |
| Platanaceae | | | | | |
| *Platanus* sp. | *Platanus occidentalis* | 5.4 | 21.1 | | |
| Poaceae | | | | | |
| *Phragmites* sp. | *Phragmites* | Cosmopolitan | | | |

| | | | | | |
|---|---|---|---|---|---|
| Rosaceae | | | | | |
| Rosaceae gen et. spec. indet. A | Rosaceae | Cosmopolitan | | | |
| Rosaceae gen et. spec. indet. B | Rosaceae | Cosmopolitan | | | |
| Rosaceae gen et. spec. indet. C | Rosaceae | Cosmopolitan | | | |
| *Sanguisorba* sp. | *Sanguisorba officinalis* | 1.4 | 15.8 | | |
| Salicaceae | | | | | |
| *Populus* sp. A (ex group *P. tremula* L.) | *Populus tremula* | 1.6 | 19 | –21.8 | 25.3 |
| | *Populus tremuloides* | –21.8 | 25.3 | | |
| *Salix gruberi* | *Salix caprea* | –9 | 17.8 | –9 | 23.2 |
| | *Salix scouleriana* | –5.6 | 23.2 | | |
| Sapindaceae | | | | | |
| *Acer askelssonii* | *Acer saccharum* | –1.1 | 15.8 | | |
| *Acer crenatifolium* subsp. *islandicum* | *Acer rubrum* | –1.1 | 23.8 | | |
| Smilacaceae | | | | | |
| *Smilax* sp. | *Smilax* | 3.4 | 18.8 | | |
| Trochodendraceae | | | | | |
| *Tetracentron atlanticum* | *Tetracentron sinense* | 2.2 | 19 | | |
| Ulmaceae | | | | | |
| aff. *Cedrelospermum* sp. | Extinct genus | | | | |
| *Ulmus* cf. *pyramidalis* | *Ulmus* | –1.2 | 24.3 | | |
| Valerianaceae | | | | | |
| Valerianaceae gen. et spec. indet. | *Valeriana* | Cosmopolitan | | | |
| Incertae sedis – Magnoliophyta | | | | | |
| *Dicotylophyllum* sp. A | – | – | – | | |
| Pollen type 1 | – | – | – | | |
| Pollen type 2 | – | – | – | | |
| Pollen type 3 | – | – | – | | |
| Pollen type 4 | – | – | – | | |
| Pollen type 5 | – | – | – | | |
| Pollen type 6 | – | – | – | | |
| Pollen type 7 | – | – | – | | |

(continued)

Taxa lists for 10 formations from the Cainozoic of Iceland indicating potential modern analogues and their climatic (MAT) parameters (continued)

| Tröllatunga-Gautshamar Formation TAXA | Potential modern analogue | MAT low °C | MAT high °C |
|---|---|---|---|
| Bryophyta | | | |
| *Sphagnum* sp. | *Sphagnum* | Cosmopolitan | |
| Lycopodiaceae | | | |
| *Lycopodium* sp. | *Lycopodium* | Cosmopolitan | |
| aff. *Huperzia* sp. | *Huperzia* | Cosmopolitan | |
| Osmundaceae | | | |
| *Osmunda parschlugiana* | *Osmunda regalis* | 3.2 | 23.9 |
| Polypodiopsida | | | |
| Pteridophyta gen. et spec. indet. 1 | Pteridophyta | – | |
| Equisetaceae | | | |
| *Equisetum* sp. | *Equisetum* | Cosmopolitan | |
| Polypodiaceae | | | |
| *Polypodium* sp. 1 | *Polypodium* | Cosmopolitan | |
| Polypodiaceae gen. et spec. indet. 1 | Polypodiaceae | Cosmopolitan | |
| Polypodiaceae gen. et spec. indet. 3 | Polypodiaceae | Cosmopolitan | |
| Polypodiaceae gen. et spec. indet. 4 | Polypodiaceae | Cosmopolitan | |
| Polypodiaceae gen. et spec. indet. 5 | Polypodiaceae | Cosmopolitan | |
| Ginkgoaceae | | | |
| *Ginkgo* sp. | *Ginkgo biloba* | Natural distribution unknown | |
| Pinaceae | | | |
| *Larix* sp. | *Larix* | –14.5 | 16.1 |
| *Picea* sect. *Picea* | *Picea* | –8.9 | 21.7 |
| *Pinus* sp. 2 Diploxylon | *Pinus* | –9.2 | 25.5 |
| *Pseudotsuga* sp. | *Pseudotsuga* | –3.9 | 24.8 |
| *Tsuga* sp. 1 | *Tsuga diversifolia* | 6.2 | 17.2 |
| Sciadopityaceae | | | |
| *Sciadopitys* sp. | *Sciadopitys verticillata* | 7.4 | 16.6 |

| | | | | | |
|---|---|---|---|---|---|
| Apiaceae | | | | | |
| Apiaceae gen. et spec. indet. 1 | Apiaceae | Cosmopolitan | | | |
| Apiaceae gen. et spec. indet. 2 | Apiaceae | Cosmopolitan | | | |
| Asteraceae | | | | | |
| *Artemisia* sp. 1 | *Artemisia* | Cosmopolitan | | | |
| *Artemisia* sp. 2 | *Artemisia* | Cosmopolitan | | | |
| Asteraceae gen. et spec. indet. 1 | Asteraceae | Cosmopolitan | | | |
| Asteraceae gen. et spec. indet. 2 | Asteraceae | Cosmopolitan | | | |
| Asteraceae gen. et spec. indet. 3 | Asteraceae | Cosmopolitan | | | |
| Betulaceae | | | | | |
| *Alnus cecropiifolia* | *Alnus glutinosa* | –3.3 | 17.4 | –3.3 | 22.4 |
| | *Alnus nitida* | 5.6 | 22.4 | | |
| | *Alnus rhombifolia* | 0 | 16.3 | | |
| *Betula islandica* | *Betula ermannii* | –7 | 14.6 | –7 | 22.5 |
| | *Betula delavayi* | 4.1 | 15.3 | | |
| | *Betula utilis* | –0.4 | 22.5 | | |
| *Carpinus* sp. | *Carpinus betulus* | 4.3 | 15.5 | 2.5 | 28.2 |
| | *Carpinus caroliniana* | 2.5 | 28.2 | | |
| | *Carpinus cordata* | 3 | 16.7 | | |
| *Corylus* sp. | *Corylus americana* | –0.4 | 17.9 | –2.7 | 19 |
| | *Corylus avellana* | 1.3 | 19 | | |
| | *Corylus chinensis* | –2.7 | 18.4 | | |
| Calycanthaceae | | | | | |
| aff. Calycanthaceae | *Calycanthus chinensis* | 11.5 | 13.4 | 5.3 | 20 |
| | *Calycanthus floridus* | 8.7 | | | |
| | *Calycanthus occidentalis* | 5.3 | 19.4 | | |
| | *Chimonanthus* spp. | 7 | 18.3 | | |
| | | | 20 | | |

(continued)

Taxa lists for 10 formations from the Cainozoic of Iceland indicating potential modern analogues and their climatic (MAT) parameters (continued)

| Tröllatunga-Gautshamar Formation TAXA | Potential modern analogue | MAT low °C | MAT high °C | | |
|---|---|---|---|---|---|
| Caprifoliaceae | | | | | |
| *Lonicera* sp. 1 | *Lonicera xylosteum* | 0.1 | 14.9 | | |
| *Lonicera* sp. 2 | | | | | |
| Caryophyllaceae | | | | | |
| Caryophyllaceae gen et. epec. indet. 1 | Caryophyllaceae | Cosmopolitan | | | |
| Caryophyllaceae gen et. epec. indet. 2 | Caryophyllaceae | Cosmopolitan | | | |
| Caryophyllaceae gen et. epec. indet. 3 | Caryophyllaceae | Cosmopolitan | | | |
| Chenopodiaceae | | | | | |
| aff. *Chenopodium* sp. | *Chenopodium* | Cosmopolitan | | | |
| Chenopodiaceae gen. et spec. indet. 1 | Chenopodiaceae | Cosmopolitan | | | |
| Cyperaceae | | | | | |
| Cyperaceae gen. et spec. indet. A | Cyperaceae | Cosmopolitan | | | |
| Ericaceae | | | | | |
| *Arctostaphylos* sp. | *Arctostaphylos* | –11.9 | 21.4 | | |
| *Rhododendron* aff. *ponticum* | *Rhododendron ponticum* | 4.1 | 18.3 | | |
| *Vaccinium* sp. | *Vaccinium* | –12.4 | 20.8 | | |
| Ericaceae gen. et spec. indet. 1 | Ericaceae | Cosmopolitan | | | |
| Fagaceae | | | | | |
| *Fagus* sp. | *Fagus sylvatica* | 5.9 | 15.7 | 5.9 | 16.7 |
| | *Fagus longipetiolata* | 6 | 16.7 | | |
| *Trigonobalanopsis* sp. | Extinct genus | | | | |
| Juglandaceae | | | | | |
| *Cyclocarya* sp. | *Cyclocarya paliurus* | 3.5 | 20.5 | | |
| *Pterocarya* sp. | *Pterocarya fraxinifolia* | 8.1 | 18.1 | –1.9 | 19.8 |
| | *Pterocarya macrocarpa* | –1.9 | 19.8 | | |
| Lemnaceae (syn. Lemnaoideae in Araceae) | | | | | |
| Lemnaceae gen. et spec. indet. | Lemnaceae | Cosmopolitan | | | |

| | | | | | |
|---|---|---|---|---|---|
| Liliaceae | | | | | |
| Liliaceae gen. et spec. indet. 1 | Liliaceae | Cosmopolitan | | | |
| Liliaceae gen. et spec. indet. 2 | Liliaceae | Cosmopolitan | | | |
| Lythraceae | | | | | |
| *Decodon* sp. | *Decodon verticillatus* | 2.1 | 19.8 | | |
| Nymphaeaceae | | | | | |
| cf. *Nuphar* sp. | *Nuphar* | Temperate northern hemisphere | | | |
| Plantaginaceae | | | | | |
| aff. *Plantago lanceolata* | *Plantago lanceolata* | Cosmopolitan | | | |
| Platanaceae | | | | | |
| *Platanus* sp. | *Platanus occidentalis* | 5.4 | 21.1 | | |
| Poaceae | | | | | |
| Poaceae gen. et spec. indet. 1 | Poaceae | Cosmopolitan | | | |
| Polygonaceae | | | | | |
| *Polygonum* sect. *Aconogonon* sp. | *Polygonum* | Cosmopolitan | | | |
| *Rumex* sp. | *Rumex* | Northern hemisphere | | | |
| Ranunculaceae | | | | | |
| *Anemone* ps. | *Anemone* | Cosmopolitan | | | |
| *Ranunculus* sp. 1 | *Ranunculus* | Cosmopolitan | | | |
| *Thalictrum* sp. 1 | *Thalictrum* | Cosmopolitan | | | |
| Ranunculaceae gen. et spec. indet. 1 | Ranunculaceae | Cosmopolitan | | | |
| Ranunculaceae gen. et spec. indet. 2 | Ranunculaceae | Cosmopolitan | | | |
| Rosaceae | | | | | |
| Rosaceae gen. et spec. indet. type A | Rosaceae | Cosmopolitan | | | |
| *Sanguisorba* sp. | *Sanguisorba officinalis* | 1.4 | 15.8 | | |
| Salicaceae | | | | | |
| *Salix gruberi* | *Salix caprea* | –9 | 17.8 | –9 | 23.2 |
| | *Salix scouleriana* | –5.6 | 23.2 | | |

(continued)

Taxa lists for 10 formations from the Cainozoic of Iceland indicating potential modern analogues and their climatic (MAT) parameters (continued)

| Tröllatunga-Gautshamar Formation TAXA | Potential modern analogue | MAT low °C | MAT high °C | | |
|---|---|---|---|---|---|
| Sapindaceae | | | | | |
| *Acer askelssonii* | *Acer saccharum* | –1.1 | 15.8 | | |
| *Acer crenatifolium* subsp. *islandicum* | *Acer rubrum* | –1.1 | 23.8 | | |
| Smilacaceae | | | | | |
| *Smilax* sp. | *Smilax* | 3.4 | 18.8 | | |
| Tiliaceae | | | | | |
| *Tilia* sp. | *Tilia americana* | 1.1 | 16.1 | 1.1 | 16.1 |
| | *Tilia platyphyllos* | 3.4 | 14 | | |
| Trochodendraceae | | | | | |
| *Tetracentron atlanticum* | *Tetracentron sinense* | 2.2 | 19 | | |
| Umaceae | | | | | |
| *Ulmus* sp. | *Ulmus* | –1.2 | 24.3 | | |
| Vitaceae | | | | | |
| *Parthenocissus* sp. | *Parthenocissus quinquefolia* | 2.1 | 19.8 | 2.1 | 21.4 |
| | *Parthenocissus heterophylla* | 9.3 | 21.4 | | |
| Incertae sedis-Magnoliophyta | | | | | |
| *Dicotylophyllum* sp. B | – | – | – | | |
| *Dicotylophyllum* sp. C | | | | | |
| Pollen type 8 | – | – | – | | |
| Pollen type 9 | – | – | – | | |
| Pollen type 10 | – | – | – | | |
| Pollen type 11 | – | – | – | | |
| Pollen type 12 | – | – | – | | |
| Pollen type 13 | – | – | – | | |
| Pollen type 14 | – | – | – | | |
| Pollen type 15 | – | – | – | | |
| Pollen type 16 | – | – | – | | |

| | | | |
|---|---|---|---|
| Pollen type 17 | – | – | – |
| Pollen type 18 | – | – | – |
| Pollen type 19 | – | – | – |
| Pollen type 20 | – | – | – |

| Skarðsströnd-Mókollsdalur Formation TAXA | Potential modern analogue | MAT low °C | MAT high °C |
|---|---|---|---|
| Lycopodiaceae | | | |
| *Lycopodiella* sp. | *Lycopodiella* | Cosmopolitar | |
| *Lycopodium* sp. | *Lycopodium* | Cosmopolitar | |
| aff. *Huperzia* sp. | *Huperzia* | Cosmopolitar | |
| Osmundaceae | | | |
| *Osmunda* sp. | *Osmunda regalis* | 3.2 | 23.9 |
| Polypodiaceae | | | |
| Polypodiaceae gen. et spec. indet. 1 | Polypodiaceae | Cosmopolitan | |
| Polypodiaceae gen. et spec. indet. 6 | Polypodiaceae | Cosmopolitan | |
| Incertae sedis – unassigned spores | | | |
| Monolete spore, fam., gen. et spec. indet. 1 | – | | |
| Monolete spore, fam., gen. et spec. indet. 2 | – | | |
| Pinaceae | | | |
| *Larix* sp. | *Larix* | –14.5 | 16.1 |
| *Picea* sect. *Picea* | *Picea* | –8.9 | 21.7 |
| *Pinus* sp. 2 Diploxylon | *Pinus* | –9.2 | 25.5 |
| *Pseudotsuga* sp. | *Pseudotsuga* | –3.9 | 24.8 |
| *Tsuga* sp. 1 | *Tsuga diversifolia* | 6.2 | 17.2 |
| *Tsuga* sp. 2 | *Tsuga* | 1.8 | 21.9 |
| Sciadopityaceae | | | |
| *Sciadopitys* sp. | *Sciadopitys verticillata* | 7.4 | 16.6 |
| Apiaceae | | | |
| Apiaceae gen. et spec. indet. 1 | Apiaceae | Cosmopolitan | |

(continued)

Taxa lists for 10 formations from the Cainozoic of Iceland indicating potential modern analogues and their climatic (MAT) parameters (continued)

| Skarðsströnd-Mókollsdalur Formation TAXA | Potential modern analogue | MAT low °C | MAT high °C | | |
|---|---|---|---|---|---|
| Aquifoliaceae | | | | | |
| *Ilex* sp. 2 | *Ilex aquifolium* | 7.2 | 18.2 | 7.2 | 22.4 |
| | *Ilex opaca* | 7.4 | 22.4 | | |
| | *Ilex decidua* | 11.1 | 22.1 | | |
| Asteraceae | | | | | |
| Asteraceae gen. et spec. indet. 1 | Asteraceae | Cosmopolitan | | | |
| Betulaceae | | | | | |
| *Alnus cecropiifolia* | *Alnus glutinosa* | –3.3 | 17.1 | –3.3 | 22.4 |
| | *Alnus nitida* | 5.6 | 22.4 | | |
| | *Alnus rhombifolia* | 0 | 16.3 | | |
| *Betula cristata* | *Betual lenta* | 1.9 | 17.1 | –5.5 | 17.1 |
| | *Betula maximowicziana* | 3.1 | 13.5 | | |
| | *Betula papyrifera* | –5.5 | 12.5 | | |
| cf. *Carpinus* | *Carpinus betulus* | 4.3 | 15.5 | 2.5 | 28.2 |
| | *Carpinus caroliniana* | 2.5 | 28.2 | | |
| | *Carpinus cordata* | 3 | 16.5 | | |
| Calycanthaceae | | | | | |
| aff. Calycanthaceae | *Calycanthus chinensis* | 11.5 | 13.4 | 5.3 | 20 |
| | *Calycanthus floridus* | 8.7 | 19.4 | | |
| | *Calycanthus occidentalis* | 5.3 | 18.3 | | |
| | *Chimonanthus* spp. | 7 | 16.7 | | |
| Cornaceae | | | | | |
| *Cornus* sp. | *Cornus florida* | 5.5 | 22 | –8.7 | 22 |
| | *Cornus alba* | –8.7 | 19.7 | | |
| Ericaceae | | | | | |
| *Rhododendron* sp. 2 | *Rhododendron maximum* | 4.6 | 17.5 | | |

| | | | | | |
|---|---|---|---|---|---|
| Fagaceae | | | | | |
| *Fagus gussonii* | *Fagus sylvatica* | 5.9 | 15.7 | 5.9 | 16.7 |
| | *Fagus longipetiolata* | 6 | 16.7 | | |
| *Quercus* infrageneric group *Quercus* sp. 1 | *Quercus robur* | 3.3 | 15 | | |
| Juglandaceae | | | | | |
| *Cyclocarya* sp. | *Cyclocarya paliurus* | 3.5 | 20.5 | | |
| *Pterocarya* sp. | *Pterocarya fraxinifolia* | 8.1 | 18.1 | 2.5 | 19.8 |
| | *Pterocarya macrocarpa* | 2.5 | 19.8 | | |
| Myricaceae | | | | | |
| *Myrica* sp. | *Myrica gale* | 0.6 | 14.2 | 0.6 | 16.1 |
| | *Myrica pensylvanica* | 1.4 | 16.1 | | |
| Poaceae | | | | | |
| Poaceae gen. et spec. indet. 1 | Poaceae | Cosmopolitan | | | |
| Ranunculaceae | | | | | |
| *Thalictrum* sp. 2 | *Thalictrum* | Cosmopolitar | | | |
| Ranunculaceae gen. et spec. indet. 2 | Ranunculaceae | Cosmopolitan | | | |
| Salicaceae | | | | | |
| *Salix gruberi* | *Salix caprea* | –9 | 17.8 | –9 | 23.2 |
| | *Salix scouleriana* | –5.6 | 23.2 | | |
| Sapindaceae | | | | | |
| *Acer crenatifolium* subsp. *islandicum* | *Acer rubrum* | –1.1 | 23.8 | | |
| *Acer askelssonii* | *Acersaccharum* | –1.1 | 15.8 | –1.1 | 17.5 |
| | *Acer platanoides* | 2 | 15 | | |
| Trochodendraceae | | | | | |
| *Tetracentron atlanticum* | *Tetracentron sinense* | 2.2 | 19 | | |
| Ulmaceae | | | | | |
| *Ulmus* section *Ulmus* sp. | *Ulmus* | –1.2 | 24.3 | | |
| Incertae sedis – Magnoliophyta | | | | | |
| *Dicotylophyllum* sp. D | – | – | – | | |
| *Dicotylophyllum* sp. E | | | | | |
| Angiosperm fam. et gen. indet. A | – | – | – | | |

(continued)

Taxa lists for 10 formations from the Cainozoic of Iceland indicating potential modern analogues and their climatic (MAT) parameters (continued)

| Hreðavatn-Stafholt Formation TAXA | Potential modern analogue | MAT low °C | MAT high °C | | |
|---|---|---|---|---|---|
| Equisetaceae | | | | | |
| *Equisetum* sp. | *Equisetum* | Cosmopolitan | | | |
| Polypodiaceae | | | | | |
| Polypodiaceae gen.et spec. indet. 1 | Polypodiaceae | Cosmopolitan | | | |
| Polypodiaceae gen.et spec. indet. 6 | Polypodiaceae | Cosmopolitan | | | |
| Incertae sedis – unassigned spores | | | | | |
| Trilete spore, fam., gen. et spec. indet. 1 | – | | | | |
| Pinaceae | | | | | |
| *Abies steenstrupiana* | *Abies* | –6.7 | 27.4 | | |
| *Larix* sp. | *Larix* | –14.5 | 16.1 | | |
| *Picea* sect. *Picea* | *Picea* | –8.9 | 21.7 | | |
| *Pinus* sp. | *Pinus* | –9.2 | 25.5 | | |
| *Pseudotsuga* sp. | *Pseudotsuga* | –3.9 | 24.8 | | |
| *Tsuga* sp. | *Tsuga* | 1.8 | 21.9 | | |
| Betulaceae | | | | | |
| *Alnus cecropiifolia* | *Alnus glutinosa* | –3.3 | 17.4 | –3.3 | 22.4 |
| | *Alnus nitida* | 5.6 | 22.4 | | |
| | *Alnus rhombifolia* | 0 | 16.3 | | |
| *Betula cristata* | *Betula maximowicziana* | 3.1 | 13.5 | –5.5 | 13.5 |
| | *Betula papyrifera* | –5.5 | 12.5 | | |
| Calycanthaceae | | | | | |
| aff. Calycanthaceae | *Calycanthus chinensis* | 11.5 | 13.4 | 5.3 | 20 |
| | *Calycanthus floridus* | 8.7 | 19.4 | | |
| | *Calycanthus occidentalis* | 5.3 | 18.3 | | |
| | *Chimonanthus* spp. | 7 | 20 | | |
| Caryophyllaceae | | | | | |
| Caryophyllaceae gen. et spec. indet. 3 | Caryophyllaceae | Cosmopolitan | | | |

| | | | | | | |
|---|---|---|---|---|---|---|
| Ceratophyllaceae | | | | | | |
| *Ceratophyllum* sp. | *Ceratophyllum* | Cosmopolitan | | | | |
| Cyperaceae | | | | | | |
| Cyperaceae gen. et spec. indet. B | Cyperaceae | Cosmopolitan | | | | |
| Ericaceae | | | | | | |
| *Rhododendron* aff. *ponticum* | *Rhododendron ponticum* | 4.1 | 18.3 | | | |
| Fagaceae | | | | | | |
| *Fagus gussonii* | *Fagus sylvatica* | 5.9 | 15.7 | } | 5.9 | 16.7 |
| | *Fagus longipetiolata* | 6 | 16.7 | } | | |
| Juglandaceae | | | | | | |
| cf. *Cyclocarya* sp. | *Cyclocarya paliurus* | 3.5 | 20.5 | | | |
| Poaceae | | | | | | |
| *Phragmites* sp. | *Phragmites* | Cosmopolitan | | | | |
| Polygonaceae | | | | | | |
| *Persicaria* sp. aff. *P. amphibia* | *Persicaria amphibia* | Northern hemisphere | | | | |
| Rosaceae | | | | | | |
| aff. *Sorbus* sp. (‘*S. aria* type’) | *Sorbus aria* | 3 | 14.7 | | | |
| Rosaceae gen. et. spec. indet. A | Rosaceae | Cosmopolitan | | | | |
| Salicaceae | | | | | | |
| *Populus* sp. B | *Populus* | –6.7 | 26 | | | |
| *Salix gruberi* | *Salix caprea* | –9 | 17.8 | } | –9.0 | 23.2 |
| | *Salix scouleriana* | –5.6 | 23.2 | } | | |
| *Salix* sp. A | *Salix* | –9.0 | 23.2 | } | | |
| Sapindaceae | | | | | | |
| *Acer askelssonii* | *Acer saccharum* | –1.1 | 15.8 | } | –1.1 | 15.8 |
| | *Acer platanoides* | 2 | 15 | } | | |
| Scrophulariaceae | | | | | | |
| aff. *Euphrasia* vel *Melampyrum* sp. | *Euphrasia, Melampyrum* | Cosmopolitan | | | | |
| Trochodendraceae | | | | | | |
| *Tetracentron atlanticum* | *Tetracetron sinense* | 2.2 | 19 | | | |
| Incertae sedis – Magnoliophyta | – | – | – | | | |
| Angiosperm fam. gen. et spec. indet. B | – | – | – | | | |

(continued)

Taxa lists for 10 formations from the Cainozoic of Iceland indicating potential modern analogues and their climatic (MAT) parameters (continued)

| Fnjóskadalur Formation TAXA | Potential modern analogue | MAT low °C | MAT high °C |
|---|---|---|---|
| Bryophyta | | | |
| *Sphagnum* sp. | *Sphagnum* | Cosmopolitan | |
| Equisetaceae | | | |
| *Equisetum* sp. | *Equisetum* | Cosmopolitan | |
| Lycopodiaceae | | | |
| *Lycopodium* | *Lycopodium* | Cosmopolitan | |
| Polypodiaceae | | | |
| Polypodiaceae gen. et spec. indet. 1 | Polypodiaceae | Cosmopolitan | |
| Polypodiaceae gen. et spec. indet. 7 | Polypodiaceae | Cosmopolitan | |
| Polypodiaceae gen. et spec. indet. 8 | Polypodiaceae | Cosmopolitan | |
| Incertae sedis – unassigned spores | | | |
| Trilete spore, fam., gen. et spec. indet. 2 | – | | |
| Pinaceae | | | |
| *Abies steenstrupiana* | *Abies* | –6.7 | 27.4 |
| *Cathaya* sp. | *Cathaya argyrophylla* | 9.3 | 18.6 |
| *Picea* sect. *Picea* | *Picea* | –8.9 | 21.7 |
| *Pinus* sp. 2 | *Pinus* | –9.2 | 25.5 |
| *Pseudotsuga/Larix* sp. | *Pseudotsuga/Larix* | –14.5 | 21.7 |
| Sciadopityaceae | | | |
| *Sciadopitys* sp. | *Sciadopitys verticillata* | 7.4 | 16.6 |
| Apiaceae | | | |
| Apiaceae gen. et. spec indet. 1 | Apiaceae | Cosmopolitan | |
| Asteraceae | | | |
| *Artemisia* sp. 1 | *Artemisia* | Cosmopolitan | |
| *Artemisia* sp. 2 | | | |
| Asteraceae gen. et spec. indet. 1 | Asteraceae | Cosmopolitan | |

| | | | | | |
|---|---|---|---|---|---|
| Asteraceae gen. et spec. indet. 2 | | | | | |
| Asteraceae gen. et spec. indet. 4 | | | | | |
| Betulaceae | | | | | |
| *Alnus cecropiifolia* | *Alnus glutinosa* | –3.3 | 17.4 | –3.3 | 22.4 |
| | *Alnus nitida* | 5.6 | 22.4 | | |
| | *Alnus rhombifolia* | 0 | 16.3 | | |
| *Betula cristata* | *Betula maximowicziana* | 3.1 | 13.5 | –5.5 | 13.5 |
| | *Betula papyrifera* | –5.5 | 12.5 | | |
| *Betula* sp. A (section *Betulaster*) | *Betula luminifera* | 1.4 | 16.9 | | |
| Calycanthaceae | | | | | |
| aff. Calycanthaceae | *Calycanthus chinensis* | 11.5 | 13.4 | 5.3 | 20 |
| | *Calycanths floridus* | 8.7 | 19.4 | | |
| | *Calycanthus occidentalis* | 5.3 | 18.3 | | |
| | *Chimonanthus* spp. | 7 | 20 | | |
| Caryophyllaceae | | | | | |
| Caryophyllaceae gen. et spec. indet. 4 | Caryophyllaceae | Cosmopolitan | | | |
| Ericaceae | | | | | |
| Ericaceae gen. et spec. indet. 2 | Ericaceae | Cosmopolitan | | | |
| Ericaceae gen. et spec. indet. 3 | Ericaceae | Cosmopolitan | | | |
| Fagaceae | | | | | |
| *Quercus* infrageneric group *Quercus* sp. 2 | *Quercus rubra* | –1.1 | 19.4 | | |
| Haloragidaceae | | | | | |
| *Myriophyllum* sp. | *Myriophyllum* | Cosmopolitan | | | |
| Liliaceae | | | | | |
| Liliaceae gen. et spec. indet. 3 | Liliaceae | Cosmopolitan | | | |

(continued)

Taxa lists for 10 formations from the Cainozoic of Iceland indicating potential modern analogues and their climatic (MAT) parameters (continued)

| Fnjóskadalur Formation TAXA | Potential modern analogue | MAT low °C | MAT high °C |
|---|---|---|---|
| Menyanthaceae | | | |
| *Menyanthes* sp. | *Menyanthes trifoliata* | Northern temperate and circumpolar | |
| Nymphaceae | | | |
| *Nuphar* sp. | *Nuphar* | Temperate northern hemisphere | |
| Plantaginaceae | | | |
| aff. *Plantago lanceolata* | *Plantago lanceolata* | Cosmopolitan | |
| Poaceae | | | |
| *Phragmites* sp. | *Phragmites* | Cosmopolitan | |
| Poaceae gen. et spec. indet. 2 | Poaceae | Cosmopolitan | |
| Poales | | | |
| Poales fam., gen. et spec. indet. | Poales | Cosmopolitan | |
| Polygonaceae | | | |
| *Polygonum viviparum* | *Polygonum viviparum* | Circumpolar | |
| Ranunculaceae | | | |
| *Ranunculus* sp. 1 | Ranunculus | Cosmopolitan | |
| *Ranunculus* sp. 2 | Ranunculus | Cosmopolitan | |
| *Thalictrum* sp. 1 | *Thalictrum* | Cosmopolitan | |
| Ranunculaceae gen. et spec. indet. 2 | Ranunculaceae | Cosmopolitan | |
| Ranunculaceae gen. et spec. indet. 3 | Ranunculaceae | Cosmopolitan | |

| | | | |
|---|---|---|---|
| Rosaceae | | | |
| *Sanguisorba* sp. | *Sanguisorba officinalis* | 1.4 | 15.8 |
| Rosaceae gen. et spec. indet. 10 | Rosaceae | Cosmopolitan | |
| Rosaceae gen. et spec. indet. 11 | Rosaceae | Cosmopolitan | |
| Salicaceae | | | |
| *Salix gruberi* | *Salix caprea* | –9 | 17.8 |
| | *Salix scouleriana* | –5.6 | 23.2 |
| *Salix* sp. A | *Salix* | –9 | 23.2 |
| Sparganiaceae | | | |
| *Sparganium* sp. | *Sparganium* | Cosmopolitan | |
| Trochodendraceae | | | |
| *Tetracentron atlanticum* | *Tetracentron sinense* | 2.2 | 19 |
| Valerianaceae | | | |
| aff. *Valeriana* sp. | *Valeriana* | Cosmopolitan | |
| Incertae sedis – Magnoliophyta | | | |
| Pollen type 21 | – | – | – |
| Pollen type 22 | – | – | – |
| Pollen type 23 | – | – | – |

(continued)

Taxa lists for 10 formations from the Cainozoic of Iceland indicating potential modern analogues and their climatic (MAT) parameters (continued)

| Tjörnes beds TAXA | Potential modern analogue | MAT low ºC | MAT high ºC |
|---|---|---|---|
| Bryophyta | | | |
| *Sphagnum* sp. | *Sphagnum* | Cosmopolitan | |
| Equisetaceae | | | |
| *Equisetum* sp. | *Equisetum* | Cosmopolitan | |
| Lycopodiaceae | | | |
| *Lycopodiella* sp. | *Lycopodiella* | Cosmopolitan | |
| *Lycopodium* sp. | *Lycopodium* | Cosmopolitan | |
| aff. *Huperzia* sp. | *Huperzia* | Cosmopolitan | |
| Lycopodiaceae gen. et. spec. indet. 1 | Lycopodiaceae | Cosmopolitan | |
| Selaginellaceae | | | |
| *Selaginella* sp. | *Selaginella* | Cosmopolitan | |
| Osmundaceae | | | |
| *Osmunda* sp. | *Osmunda regalia* | 3.2 | 23.9 |
| Polypodiaceae | | | |
| *Polypodium* sp. 1 | *Polypodium* | Cosmopolitan | |
| Polypodiaceae gen. et. spec. indet. 1 | Polypodiaceae | Cosmopolitan | |
| Polypodiaceae gen. et spec. indet. 2 | Polypodiaceae | Cosmopolitan | |
| Polypodiaceae gen. et spec. indet. 6 | Polypodiaceae | Cosmopolitan | |
| Incertae sedis – unassigned spores | | | |
| Trilete spore, fam., gen. et spec. indet. 3 | – | – | – |
| Trilete spore, fam., gen. et spec. indet. 4 | – | – | – |
| Trilete spore, fam., gen. et. spec. indet. 5 | – | – | – |
| Monolete spore, fam., gen. spec. indet. 3 | – | – | – |
| Monolete spore, fam., gen. et spec. indet. 4 | – | – | – |
| Pinaceae | | | |
| *Abies* sp. 2 | *Abies* | –6.7 | 27.4 |
| *Picea* sp. | *Picea* | –8.9 | 21.7 |

| | | | | | |
|---|---|---|---|---|---|
| *Pinus* sp. 2 | *Pinus* | –9.2 | 25.5 | | |
| *Larix* sp. | *Larix* | –14.5 | 16.1 | | |
| *Tsuga* sp. 1 | *Tsuga* | 1.8 | 21.9 | | |
| Sciadopityaceae | | | | | |
| *Sciadopitys* sp. | *Sciadopitys verticillata* | 7.4 | 16.6 | | |
| Apiaceae | | | | | |
| Apiaceae gen. et spec. indet. 1 | Apiaceae | Cosmopolitan | | | |
| Apiaceae gen. et spec. indet. 2 | Apiaceae | Cosmopolitan | | | |
| Apiaceae gen. et spec. indet. 3 | Apiaceae | Cosmopolitan | | | |
| Aquifoliaceae | | | | | |
| *Ilex* sp. 1 | *Ilex aquifolium* | 7.2 | 18.2 | 7.2 | 22.4 |
| | *Ilex opaca* | 7.4 | 22.4 | | |
| | *Ilex decidua* | 11.1 | 22.1 | | |
| Araceae | | | | | |
| aff. *Arum* sp. | *Arum* | Northern hemispheric | | | |
| Asteraceae | | | | | |
| *Cirsium* sp. | | | | | |
| Asteraceae gen. et spec. indet. 1 | Asteraceae | Cosmopolitan | | | |
| Asteraceae gen. et spec. indet. 5 | Asteraceae | Cosmopolitan | | | |
| Asteraceae gen. et spec. indet. 6 | Asteraceae | Cosmopolitan | | | |
| Asteraceae gen. et spec. indet. 7 | Asteraceae | Cosmopolitan | | | |
| Asteraceae gen. et spec. indet. 8 | Asteraceae | Cosmopolitan | | | |
| Betulaceae | | | | | |
| *Alnus cecropiifolia* | *Alnus glutinosa* | –3.3 | 17.4 | –3.3 | 22.4 |
| | *Alnus nitida* | 5.6 | 22.4 | | |
| | *Alnus rhombifolia* | 0 | 16.3 | | |
| *Alnus* aff. *viridis* | *Alnus viridis* | Temperate and subarctic northern hemisphere | | | |
| *Betula* sp. | *Betula* | | | | |

(continued)

Taxa lists for 10 formations from the Cainozoic of Iceland indicating potential modern analogues and their climatic (MAT) parameters (continued)

| Tjörnes beds TAXA | Potential modern analogue | MAT low ºC | MAT high ºC | | |
|---|---|---|---|---|---|
| Calycanthaceae | | | | | |
| aff. Calycanthaceae | *Calycanthus chinensis* | 11.5 | 13.4 | 5.3 | 20 |
| | *Calycanthus floridus* | 8.7 | 19.4 | | |
| | *Calycanthus occidentalis* | 5.3 | 18.3 | | |
| | *Chimonanthus* spp. | 7 | 20 | | |
| Campanulaceae | | | | | |
| *Campanula* sp. | *Campanula* | Northern hemispheric | | | |
| Caryophyllaceae | | | | | |
| Caryophyllaceae gen. et spec. indet. 1 | Caryophyllaceae | Cosmopolitan | | | |
| Caryophyllaceae gen. et spec. indet. 4 | Caryophyllaceae | Cosmopolitan | | | |
| Caryophyllaceae gen. et spec. indet. 5 | Caryophyllaceae | Cosmopolitan | | | |
| Chenopodiaceae | | | | | |
| aff. *Chenopodium* sp. | *Chenopodium* | Cosmopolitan | | | |
| Cyperaceae | | | | | |
| *Carex* sp. | *Carex* | Cosmopolitan | | | |
| *Kobresia* sp. | *Kobresia* | Northern hemisphere high mountain areas | | | |
| Ericaceae | | | | | |
| *Rhododendron* aff. *ponticum* | *Rhododendron ponticum* | 4.1 | 18.3 | | |
| *Rhododendron* sp. 2 | *Rhododendron maximum* | 4.6 | 17.5 | | |
| *Vaccinium* cf. *uliginosum* | *Vaccinium uliginosum* | Temperate and subarctic northern hemisphere | | | |
| Ericaceae gen. et spec. indet. 4 | Ericaceae | Cosmopolitan | | | |
| Ericaceae gen. et spec. indet. 5 | Ericaceae | Cosmopolitan | | | |
| Ericaceae gen. et spec. indet. 6 | Ericaceae | Cosmopolitan | | | |
| Ericaceae gen. et spec. indet. 7 | Ericaceae | Cosmopolitan | | | |

| | | | | | | |
|---|---|---|---|---|---|---|
| Euphorbiaceae | | | | | | |
| *Euphorbia* sp. | *Euphorbia cyparissias* | 1 | 11.1 | | | |
| Fagaceae | | | | | | |
| *Trigonobalanopsis* sp. | Extinct genus | | | | | |
| Juglandaceae | | | | | | |
| *Pterocarya* sp. | *Pterocarya fraxinifolia* | 8.1 | 18.1 | } | | |
| | *Pterocarya macroptera* | –1.9 | | | –1.9 | 19.8 |
| | | | 19.8 | } | | |
| Haloragidaceae | | | | | | |
| *Myriophyllum* sp. | *Myriophyllum* | Cosmopolitan | | | | |
| Liliaceae | | | | | | |
| Liliaceae gen. et spec. indet. 3 | Liliaceae | Cosmopolitan | | | | |
| Menyanthaceae | | | | | | |
| *Menyanthes* sp. | *Menyanthes trifoliata* | Northern temperate and circumpolar | | | | |
| Myricaceae | | | | | | |
| *Myrica* sp. | *Myrica gale* | 0.6 | 14.2 | | | |
| Onagraceae | | | | | | |
| *Epilobium* sp. | *Epilobium* | Cosmopolitan | | | | |
| Plantaginaceae | | | | | | |
| *Plantago coronopus* | *Plantago coronopus* | Sahara to Scandinavia and the Faeroe | | | | |
| Poaceae | | Islands, edaphically controlled | | | | |
| *Phragmites* sp. | *Phargmites* | Cosmopolitan | | | | |
| Poaceae gen. et spec. indet. 1 | Poaceae | Cosmopolitan | | | | |
| Poaceae gen. et spec. indet. 3 | Poaceae | Cosmopolitan | | | | |

(continued)

Taxa lists for 10 formations from the Cainozoic of Iceland indicating potential modern analogues and their climatic (MAT) parameters (continued)

| Tjörnes beds TAXA | Potential modern analogue | MAT low ºC | | MAT high ºC | | |
|---|---|---|---|---|---|---|
| Polygonaceae | | | | | | |
| *Rumex* sp. | *Rumex* | Northern hemisphere | | | | |
| *Persicaria* sp. aff. *P. amphibia* | *Persicaria amphibia* | Northern hemisphere | | | | |
| *Polygonum viviparum* | *Polygonum viviparum* | Circumpolar | | | | |
| Potamogetonaceae | | | | | | |
| *Potamogeton* sp. | *Potamogeton* | Cosmopolitan | | | | |
| Ranunculaceae | | | | | | |
| *Ranunculus* sp. 1 | *Ranunculus* | Cosmopolitan | | | | |
| *Ranunculus* sp. 2 | *Ranunculus* | Cosmopolitan | | | | |
| *Thalictrum* sp. 2 | *Thalictrum* | Cosmopolitan | | | | |
| Ranunculaceae gen. et spec. indet. 2 | Ranunculaceae | Cosmopolitan | | | | |
| Ranunculaceae gen. et spec. indet. 4 | Ranunculaceae | Cosmopolitan | | | | |
| Ranunculaceae gen. et spec. indet. 5 | Ranunculaceae | Cosmopolitan | | | | |
| Rosaceae | | | | | | |
| *Filipendula* sp. | *Filipendula* | Northern temperate | | | | |
| *Fragaria* sp. 1 | *Fragaria* | Cosmopolitan | | | | |
| *Fragaria* sp. 2 | | | | | | |
| *Sanguisorba* sp. | *Sanguisorba officinalis* | 1.4 | 15.8 | | | |
| *Sorbus* aff. *aucuparia* | *Sorbus aucuparia* | –2.1 | 14.7 | | | |
| | *Sorbus americana* | –15.1 | 15.7 | | –6.2 | 15.7 |
| | *Sorbus decora* | –6.2 | 9.8 | | | |
| Rosaceae gen. et spec. indet. 11 | Rosaceae | Cosmopolitan | | | | |
| Rosaceae gen. et spec. indet. 12 | Rosaceae | Cosmopolitan | | | | |

| | | | | | | |
|---|---|---|---|---|---|---|
| Salicaceae | | | | | | |
| *Salix gruberi* | *Salix caprea* | –9 | 17.8 | } | –9 | 23.2 |
| | *Salix scouleriana* | –5.6 | 23.2 | } | | |
| *Salix* sp. B (‘S. *arctica*’ type) | *Salix arctica* | –18.2 | 5.5 | } | –18.2 | 8.5 |
| | *Salix lanata* | –7.3 | 8.5 | } | | |
| *Salix* sp. 4 | *Salix caprea* | –9 | 17.8 | | | |
| Sapindaceae | | | | | | |
| *Acer* sp. 1 | *Acer saccharum* | –1.1 | 15.8 | | | |
| *Acer* sp. 2 | *Acer rubrum* | –1.1 | 23.8 | | | |
| Sparganiaceae | | | | | | |
| *Sparganium* sp. | *Sparganium* | Cosmopolitan | | | | |
| Trochodendraceae | | | | | | |
| *Tetracentron atlanticum* | *Tetracentron sinense* | 2.2 | 19 | | | |
| Valerianaceae | | | | | | |
| aff. *Valeriana* sp. | *Valeriana* | Cosmopolitan | | | | |
| Viscaceae | | | | | | |
| *Viscum* aff. *album* | *Viscum album* | 5.2 | 17.4 | | | |
| Incertae sedis – Magnoliophyta | | | | | | |
| Monocotyledonae fam.et gen. indet. 1 | – | – | – | | | |
| Angiosperm fam. gen. et spec. indet. C | – | – | – | | | |
| Pollen type 24 | – | – | – | | | |
| Pollen type 25 | – | – | – | | | |
| Pollen type 26 | – | – | – | | | |
| Pollen type 27 | – | – | – | | | |
| Pollen type 28 | – | – | – | | | |
| Pollen type 29 | – | – | – | | | |
| Pollen type 30 | – | – | – | | | |

(continued)

Taxa lists for 10 formations from the Cainozoic of Iceland indicating potential modern analogues and their climatic (MAT) parameters (continued)

| Viðidalur Formation TAXA | Potential modern analogue | MAT low °C | MAT high °C | | |
|---|---|---|---|---|---|
| Bryophyta | | | | | |
| *Sphagnum* sp. | *Sphagnum* | Cosmopolitan | | | |
| Lycopodiaceae | | | | | |
| *Lycopodium* sp. | *Lycopodium* | Cosmopolitan | | | |
| aff. *Huperzia* sp. | *Huperzia* | Cosmopolitan | | | |
| Osmundaceae | | | | | |
| *Osmunda* sp. | *Osmunda regalis* | 3.2 | 23.9 | | |
| Polypodiaceae | | | | | |
| Polypodiaceae gen. et spec. indet. 1 | Polypodiaceae | Cosmopolitan | | | |
| Incertae sedis - unassigned spores | | | | | |
| Trilete spore, fam., gen. et spec. indet. 6 | - | | | | |
| Trilete spore, fam., gen. et spec. indet. 7 | - | | | | |
| Pinaceae | | | | | |
| *Pinus* sp. 2 Diploxylon | *Pinus* | -9.2 | 25.5 | | |
| Asteraceae | | | | | |
| *Artemisia* sp. 1 | *Artemisia* | Cosmopolitan | | | |
| Asteraceae gen. et spec. indet. 1 | Asteraceae | Cosmopolitan | | | |
| Betulaceae | | | | | |
| *Alnus* aff. *viridis* | *Alnus viridis* | -12.4 | 12.3 | | |
| *Betula nana* x *pubescens* | *Betula nana* | -12.4 | 14.3 | 12.4 | 14.3 |
| | *Betula pubescens* | -2.3 | 14.2 | | |
| Caryophyllaceae | | | | | |
| Caryophyllaceae gen. et spec. indet. 4 | Caryophyllaceae | Cosmopolitan | | | |
| Caryophyllaceae gen. et spec. indet. 6 | Caryophyllaceae | Cosmopolitan | | | |
| Caryophyllaceae gen. et spec. indet. 7 | Caryophyllaceae | Cosmopolitan | | | |
| Cyperaceae | | | | | |
| *Kobresia* sp. | *Kobresia* | Northern hemisphere high mountains | | | |

| | | | | | | |
|---|---|---|---|---|---|---|
| Ericaceae | | | | | | |
| Ericaceae gen. et spec. indet. 8 | Ericaceae | Cosmopolitan | | | | |
| *Vaccinium* cf. *uliginosum* | *Vaccinium uliginosum* | Temperate, subarctic n. hemisphere | | | | |
| Menyanthaceae | | | | | | |
| *Menyanthes* sp. | *Menyanthes* | Cosmopolitan | | | | |
| Myricaceae | | | | | | |
| *Myrica* sp. | *Myrica gale* | -1.5 | 12.3 | | | |
| Polygonaceae | | | | | | |
| *Plygonum* sect. *Aconogonon* sp. | *Polygonum* | Cosmopolitan | | | | |
| *Polygonum viviparum* | *Polygonum viviparum* | Northern hemisphere | | | | |
| *Rumex* sp. | *Rumex* | Northern hemisphere | | | | |
| Ranunculaceae | | | | | | |
| *Ranunculus* sp. 3 | *Ranunculus* | Cosmopolitan | | | | |
| *Thalictrum* sp. 2 | *Thalictrum* | Cosmopolitan | | | | |
| *Trollius* sp. | *Trollius europaeus* | -2.3 | 12.2 | | | |
| Ranunculaceae gen. et spec. indet. 2 | Ranunculaceae | Cosmopolitan | | | | |
| Ranunculaceae gen. et spec. indet. 6 | Ranunculaceae | Cosmopolitan | | | | |
| Rosaceae | | | | | | |
| *Dryas octopetala* | *Dryas octopetala* | Arctic-Alpine, northern hemisphere | | | | |
| *Fragaria* sp. 1 | *Fragaria* | Cosmopolitan | | | | |
| *Sanguisorba* sp. | *Sanguisorba officinalis* | 1.4 | 15.8 | | | |
| Rosaceae gen. et spec. indet. 13 | Rosaceae | Cosmopolitan | | | | |
| Salicaceae | | | | | | |
| *Salix* sp. B (‘*S. arctica*’ type) | *Salix arctica* | -18.2 | 5.5 | } | -18.2 | 8.5 |
| | *Salix lanata* | -7.3 | 8.5 | } | | |
| Saxifragaceae | | | | | | |
| *Saxifraga* sp. | *Saxifraga* | Arctic-Alpine | | | | |
| Incertae sedis - Magnoliophyta | | | | | | |
| Pollen type 28 | - | | | | | |

(continued)

Taxa lists for 10 formations from the Cainozoic of Iceland indicating potential modern analogues and their climatic (MAT) parameters (continued)

| Búlandshöfði Formation TAXA | Potential modern analogue | MAT low °C | MAT high °C | | | |
|---|---|---|---|---|---|---|
| Lycopodiaceae | | | | | | |
| *Lycopodium* sp. | *Lycopodium* | Cosmopolitan | | | | |
| aff. *Huperzia* sp. | *Huperzia* | Cosmopolitan | | | | |
| Lycopodiaceae gen. et spec. indet. 2 | Lycopodiaceae | Cosmopolitan | | | | |
| Osmundaceae | | | | | | |
| *Osmunda* sp. | *Osmunda regalis* | 3.2 | 23.9 | | | |
| Polypodiaceae | | | | | | |
| Polypodiaceae gen. et spec. indet. 1 | Polypodiaceae | Cosmopolitan | | | | |
| Incertae sedis – unassigned spores | | | | | | |
| Trilete spore, fam., gen. et spec. indet. 6 | – | | | | | |
| Pinaceae | | | | | | |
| *Pinus* sp. 2 Diploxylon | *Pinus* | –9.2 | 25.5 | | | |
| Asteraceae | | | | | | |
| *Artemisia* sp. 1 | *Artemisia* | Cosmopolitan | | | | |
| Asteraceae gen. et spec. indet. 1 | Asteraceae | Cosmopolitan | | | | |
| Asteraceae gen. et spec. indet. 4 | Asteraceae | Cosmopolitan | | | | |
| Asteraceae gen. et spec. indet. 8 | Asteraceae | Cosmopolitan | | | | |
| Asteraceae gen. et spec. indet. 9 | Asteraceae | Cosmopolitan | | | | |
| Asteraceae gen. et spec. indet. 10 | Asteraceae | Cosmopotian | | | | |
| Betulaceae | | | | | | |
| *Alnus* sp. 3 | *Alnus viridis* | –12.4 | 12.3 | | | |
| *Betula* sp. 1 | *Betula nana* | –12.4 | 14.3 | } | –12.4 | 14.3 |
| | *Betula pubescens* | –2.3 | 14.2 | } | | |
| Caryophyllaceae | | | | | | |
| Caryophyllaceae gen. et spec. indet. 6 | Caryophyllaceae | Cosmopolitan | | | | |
| Caryophyllaceae gen. et spec. indet. 8 | Caryophyllaceae | Cosmopolitan | | | | |
| Caryophyllaceae gen. et spec. indet. 9 | Caryophyllaceae | Cosmopolitan | | | | |
| Caryophyllaceae gen. et spec. indet. 10 | Caryophyllaceae | Cosmopolitan | | | | |

| | | | | | | |
|---|---|---|---|---|---|---|
| Empetraceae | | | | | | |
| *Empetrum nigrum* | *Empetrum nigrum* | –12.4 | 8.2 | | | |
| Ericaceae | | | | | | |
| *Vaccinium* cf. *uliginosum* | *Vaccinium uliginosum* | Temperate, subarctic n. hemisphere | | | | |
| Ericaceae gen. et spec. indet. 6 | Ericaceae | Cosmopolitan | | | | |
| Euphorbiaceae | | | | | | |
| *Mercurialis perennis* | *Mercurialis perennis* | 2.7 | 17.6 | | | |
| Onagraceae | | | | | | |
| Onagraceae gen. et spec. indet. | Onagraceae | | | | | |
| Plantaginaceae | | | | | | |
| *Plantago coronopus* | *Plantago coronopus* | Sahara to Scandinavia, Faeroe Islands | | | | |
| Poaceae | | | | | | |
| Poaceae gen. et spec. indet. 1 | Poaceae | Cosmopolitan | | | | |
| Poaceae gen. et spec. indet. 4 | Poaceae | Cosmopolitan | | | | |
| Poales | | | | | | |
| Poales gen. et spec. indet. | Poales | Cosmopolitan | | | | |
| Polygonaceae | | | | | | |
| *Polygonum aviculare* | *Polygonum aviculare* | Cosmopolitan | | | | |
| *Polygonum viviparum* | *Polygonum viviparum* | Circumpolar | | | | |
| *Rumex* sp. | | | | | | |
| Ranunculaceae | | | | | | |
| Ranunculaceae gen. et spec. indet. 2 | Ranunculaceae | Cosmopolitan | | | | |
| Rosaceae | | | | | | |
| *Potentilla* sp. A | *Potentilla* | Northern hemisphere | | | | |
| Salicaceae | | | | | | |
| *Salix* sp. B (‘*S. arctica*’ type) | *Salix arctica* | –18.2 | 5.5 | } | –18.2 | 8.5 |
| | *Salix lanata* | –7.3 | 8.5 | } | | |

(continued)

Taxa lists for 10 formations from the Cainozoic of Iceland indicating potential modern analogues and their climatic (MAT) parameters (continued)

| Búlandshöfði Formation TAXA | Potential modern analogue | MAT low °C | MAT high °C |
|---|---|---|---|
| *Salix herbacea* | *Salix herbacea* | –12.2 | 7.2 |
| Valerianaceae | | | |
| *Valeriana* sp. | *Valeriana officinalis* | 1.3 | 14.7 |
| Incertae sedis – Magnoliophyta | | | |
| Monocotyledonae fam. et gen. indet. 2 | – | – | – |
| Pollen type 28 | – | – | – |
| Pollen type 31 | – | – | – |

| Svínafellsfjall Formation TAXA | Potential modern analogue | MAT low | MAT high |
|---|---|---|---|
| Bryophytes | | | |
| *Sphagnum* sp. | *Sphagnum* | Cosmopolitan | |
| Equisetaceae | | | |
| **Equisetum** sp. | *Equisetum* | Cosmopolitan | |
| Lycopodiaceae | | | |
| *Lycopodium* sp. | *Lycopodium* | Cosmopolitan | |
| Polypodiaceae | | | |
| Polypodiaceae gen. et spec. indet. 1 | Polypodiaceae | Cosmopolitan | |
| Polypodiaceae gen. et spec. indet. A | Polypodiaceae | Cosmopolitan | |
| Thelipteridaceae | | | |
| *Thelipteris limbosperma* | *Thelipteris limbosperma* | 0.7 | 7.2 |
| Incertae sedis – unassigned spores | | | |
| Trilete spore, fam., gen. et spec. indet. 8 | – | – | – |
| Pinaceae | | | |
| *Pinus* sp. 2 Diploxylon | *Pinus* | –9.2 | 25.5 |
| Apiaceae | | | |
| Apiaceae gen. et spec. indet. 2 | Apiaceae | Cosmopolitan | |
| Asteraceae | | | |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Artemisia* sp. 1 | *Artemisia* | Cosmopolitan | | | | |
| *Artemisia* sp. 2 | *Artemisia* | Cosmopolitan | | | | |
| Asteraceae gen. et spec. indet. 3 | Asteraceae | Cosmopolitan | | | | |
| Asteraceae gen. et spec. indet. 4 | Asteraceae | Cosmopolitan | | | | |
| Asteraceae gen. et spec. indet. 8 | Asteraceae | Cosmopolitan | | | | |
| Asteraceae gen. et spec. indet. 11 | Asteraceae | Cosmopolitan | | | | |
| Asteraceae gen. et spec. indet. 12 | Asteraceae | Cosmopolitan | | | | |
| Betulaceae | | | | | | |
| *Alnus* cf. *viridis* | *Alnus viridis* | –12.4 | 12.3 | | | |
| *Betula* sp. 1 | *Betula nana* | –12.4 | 14.3 | } | –12.4 | 14.3 |
| | *Betula pubescens* | –2.3 | 14.2 | } | | |
| Chenopodiaceae | | | | | | |
| Chenopodiaceae gen. et spec. indet. 2 | Chenopodiaceae | Cosmopolitan | | | | |
| Cyperaceae | | | | | | |
| Cyperaceae gen. et spec. indet. C | Cyperaceae | Cosmopolitan | | | | |
| Ericaceae | | | | | | |
| *Vaccinium* cf. *uliginosum* | *Vaccinium uliginosum* | Temperate, subarctic northern hemisphere | | | | |
| Ericaceae gen. et spec. indet. 6 | Ericaceae | Cosmopolitan | | | | |
| Ericaceae gen. et spec. indet. 9 | Ericaceae | Cosmopolitan | | | | |
| Menyanthaceae | | | | | | |
| *Menyanthes* sp. | *Menyanthes* | Cosmopolitan | | | | |
| Poaceae | | | | | | |
| Poaceae gen. et spec. indet. 4 | Poaceae | Cosmopolitan | | | | |
| Poaceae gen. et spec. indet. 5 | Poaceae | Cosmopolitan | | | | |
| Poaceae gen. et spec. indet. 6 | Poaceae | Cosmopolitan | | | | |
| Poaceae gen. et spec. indet. 7 | Poaceae | Cosmopolitan | | | | |
| Poales | | | | | | |
| Poales fam. gen. et spec. indet. | Poales | Cosmopolitan | | | | |

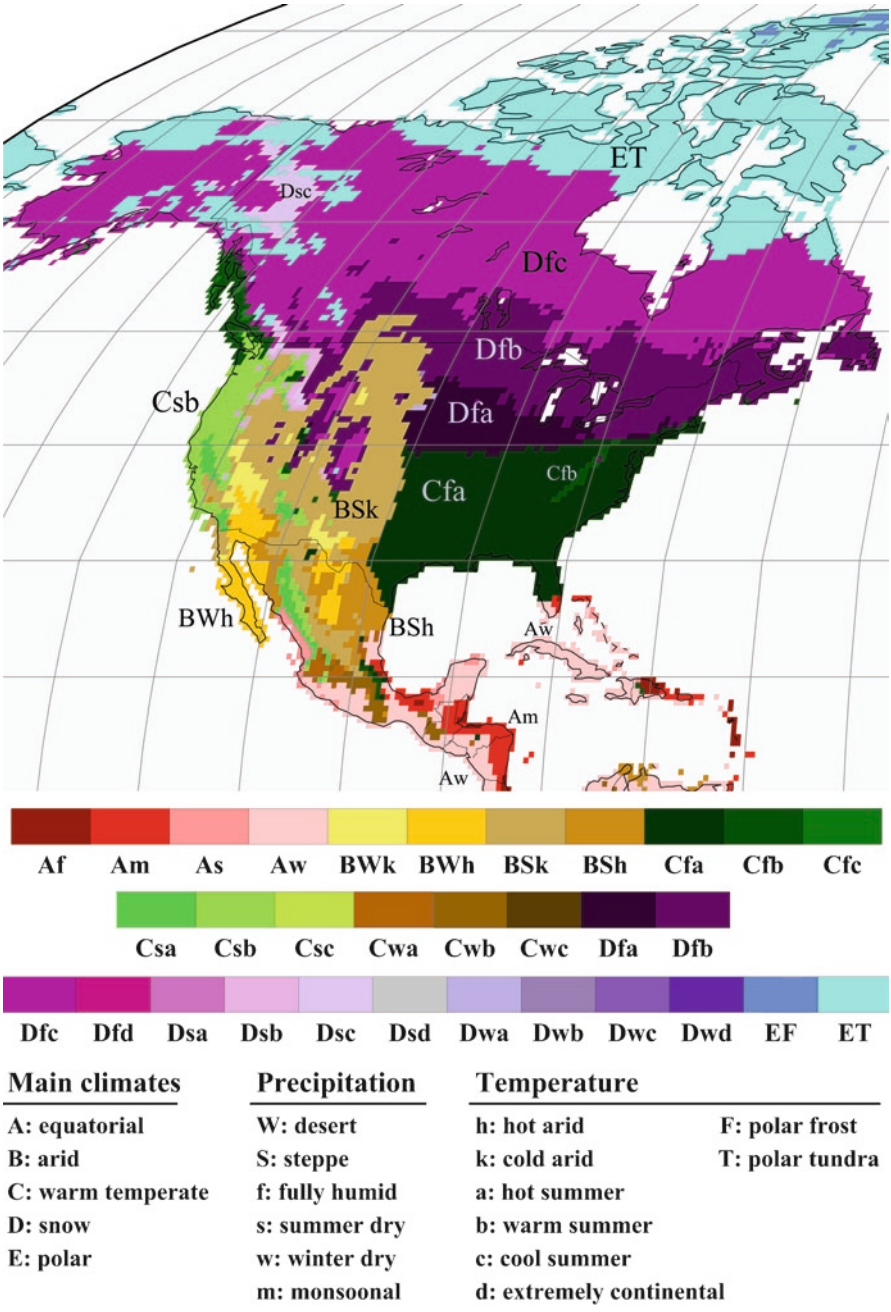
(continued)

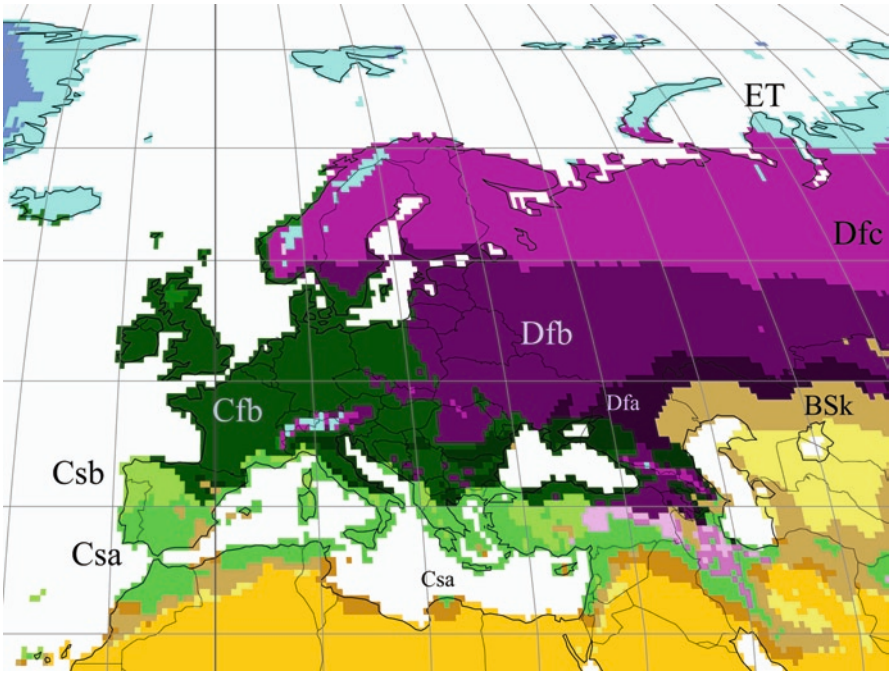
Taxa lists for 10 formations from the Cainozoic of Iceland indicating potential modern analogues and their climatic (MAT) parameters (continued)

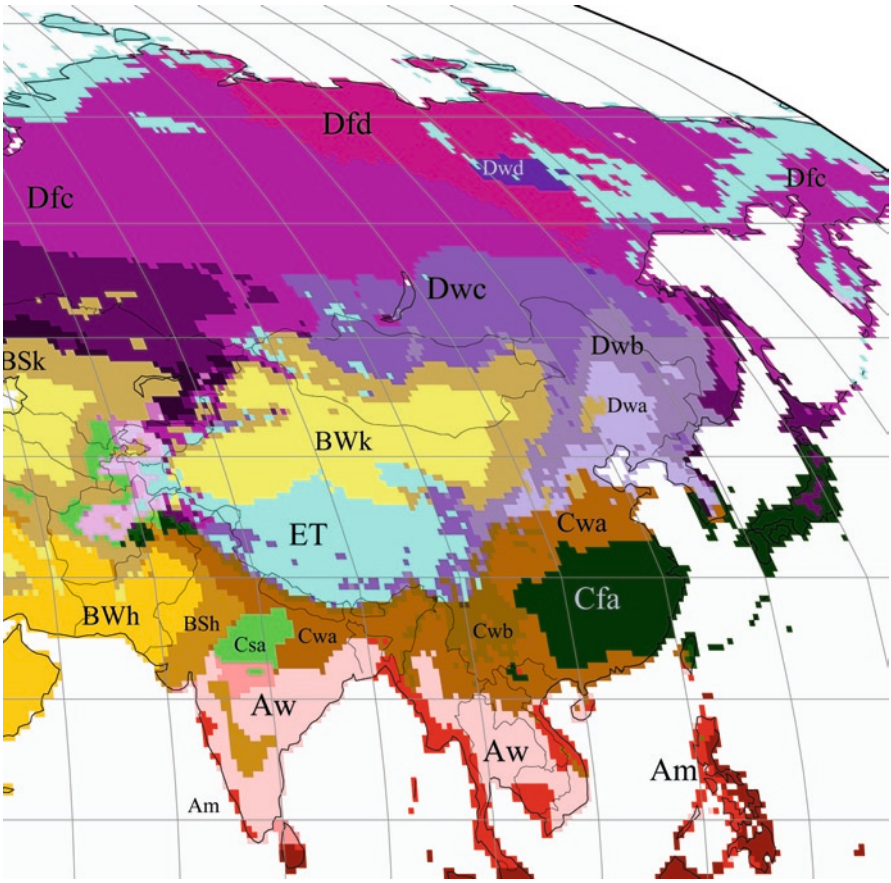
| Svínafellsfjall Formation TAXA | Potential modern analogue | MAT low | MAT high | | |
|---|---|---|---|---|---|
| Polygonaceae | | | | | |
| *Polygonum viviparum* | *Polygonum viviparum* | Circumpolar | | | |
| *Rumex* sp. | *Rumex* | Northern hemisphere | | | |
| Ranunculaceae | | | | | |
| *Thalictrum* sp. 1 | *Thalictrum* | Cosmopolitan | | | |
| *Thalictrum* sp. 2 | | | | | |
| Ranunculaceae gen. et spec. indet. 7 | Ranunculaceae | Cosmopolitan | | | |
| *Ranunculus* sp. A | *Ranunculus* | Cosmopolitan | | | |
| Rosaceae | | | | | |
| *Alchemilla* sp. | *Alchemilla vulgaris* | 1.5 | 14.2 | | |
| *Dryas octopetala* | *Dryas octopetala* | Arctic-Alpine, northern hemisphere | | | |
| *Sorbus* aff. *aucuparia* | *Sorbus aucuparia* | –2.1 | 14.7 | | |
| | *Sorbus americana* | –5.1 | 15.7 | –6.2 | 15.7 |
| | *Sorbus decora* | –6.2 | 9.8 | | |
| Rubiaceae | | | | | |
| *Galium* sp. | *Galium* | Cosmopolitan | | | |
| Salicaceae | | | | | |
| *Salix* sp. B (‘*S.* arctica’ type) | *Salix arctica* | –18.2 | 5.5 | | |
| | *Salix lanata* | –7.3 | 8.5 | –18.2 | 8.5 |
| | | | 7.2 | | |
| *Salix herbacea* | *Salix herbacea* | –12.2 | 7.2 | | |
| Scrophulariaceae | | Cosmopolitan | | | |
| Scrophulariaceae gen. et spec. indet. | Scrophulariaceae | Cosmopolitan | | | |
| Incertae sedis – Magnoliophyta | | | | | |
| Pollen type 32 | – | – | – | | |

# Appendix 13.2

Maps of Köppen-Geiger climate types for North America, western Eurasia, and Central and East Asia (from Kottek et al. 2006)




ET
Dfc
Dfb
Dfa
BSk
Cfb
Csb
Csa
Csa




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# Chapter 14
# Art Meets Science – The Unpublished Drawings by Carl Hedelin and Thérèse Ekblom

**Abstract** At the end of the nineteenth century, Alfred Gabriel Nathorst (1850–1921), then professor of palaeobotany in Stockholm, planned a major investigation of plant fossils from Iceland. This work was, however, put aside and not revived before his death. What remained was a set of more than 40 sheets containing pencil drawings of several hundred fossils from Iceland. The drawings prepared by Carl Axel Hedelin and Thérèse Ekblom between 1885 and ca 1910 are of extraordinary beauty and highest precision. Because of their grandeur and accuracy these pencil drawings constitute an outstanding body of scientific illustrations. They are made available here for the first time.

## 14.1 Scientific Illustrations in Nineteenth Century Palaeobotany

At the dawn of modern palaeobotany it was already realized that illustrations of fossil plants are of paramount importance as accompanying information to the pure description. This was in strong contrast to Linnaeus' (1737) statements on the value of illustrations. In his *Genera Plantarum*, §13, Linnaeus stated: "Icones … pro determinandis generibus non commendo, sed absolute rejicio, licet fatear has magis gratas esse pueris, iisque qui plus habent capitis quam cerebri; fateor has idiotis aliquid imponere." ("I do not recommend drawings … for determining genera, in fact, I absolutely reject them, although I confess that they are of great importance to boys and those who have more brain-pan than brain; I confess that they convey something to the unlearned." [translation by Reeds 2004]). Botanical progress, he insisted, depended on the use of clear, detailed, technical, written descriptions rather than pictures (Reeds 2004).

Early publications in palaeobotany are richly illustrated. Schlotheim (see Chap. 2), for instance, repeatedly stressed that he regarded the factual evidence provided by the descriptions *and* illustrations of the fossils as being central to his work (Cleal et al. 2005). Many scientists apparently had illustrators preparing drawings of the fossils they were describing. The accuracy and, therefore, the usefulness of these illustrations vary considerably between different works. The comparison of original fossil specimens with their illustrations reveals in some cases that the illustrations were

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oversimplified (cf. Sordelli 1896) or depicted details not visible on the original specimens (cf. Heer 1868). In the latter case, this would raise the suspicion that the illustrations were prepared not solely based upon what the illustrator saw, but were influenced by the prior interpretations of the scientist. In contrast, some pencil drawings prepared at around the same time (Nathorst 1888, 1890a, b, 1894, 1897, 1902a, b, 1906a, b, 1908a, b, c, 1909a, b; Florin 1920; Kvaček and Manum 1997) were much more accurate and equal to the precision of photographic illustrations that started to appear in Nathorst's works and elsewhere after ca 1905 (see, for example, illustrations by Hedelin and Ekblom in Nathorst 1888, 1894 and Florin 1922).

The quality of illustrations in terms of scientific value also depended on the techniques used for the reproduction. Several printing methods were available in the nineteenth century (cf. Cleal et al. 2005). Among the most common ones were intaglio printing (etching and engraving; cf. von Schlotheim 1804; Sternberg 1820–1825) and lithography (cf. Brongniart 1828; Schimper and Mougeot 1844; Unger 1847; Heer 1855–1859; Heer 1868–1883; Massalongo and Scarabelli 1859; Nathorst 1878, 1883; Renault and Zeiller 1888). At the end of the nineteenth century, lithographic printing of Nathorst's work (e.g., Nathorst 1878, 1883) was replaced by collotype (for this variant of lithography see Crawford 1982) and this was used for most of Nathorst's publications after ca 1885 (see above). This method, in combination with the outstanding drawings made by Nathorst's illustrators, especially Carl Hedelin, provided the basis for a great number of palaeobotanical illustrations that are among the best ever published. The drawings of Late Tertiary plants from Iceland presented here for the first time were meant to be printed using the collotype method but never went to the printing house. Why was this?

## 14.2 Nathorst's Plans to Publish the Tertiary Floras of Iceland

Alfred Gabriel Nathorst (1850–1921; Fig. 14.1) became the first professor at the Department of Palaeobotany at the Natural History Museum in Stockholm in 1884. Nathorst was a botanist, palaeontologist, geologist, and Arctic explorer (Liljequist 1993; Johansson 2009). Before his death, Nathorst had begun a long-term project to describe the plant fossils from the Arctic areas that was planned as a continuation of the *magnum opus* by Oswald Heer (*Flora fossilis arctica*; Heer 1868–1883). The first part of Nathorst's *Zur fossilen Flora der Polarländer* consisted of four issues (*Lieferungen*), dealing with Palaeozoic and Mesozoic Arctic floras (Nathorst 1894, 1897, 1902b, 1914). When the first issue was released, a short note appeared in the journal *Geologiska Föreningens i Stockholm Förhandlingar* (Fig. 14.2). This note and the text on the back cover of Nathorst's 1894 and 1897 publications *Zur fossilen Flora der Polarländer* clearly stated his plans to include the fossil floras from Iceland in later volumes. Also, Thoroddsen (1922–1923; Chap. 2) wrote in his memoires that Nathorst had promised to work on the large collection of Icelandic plant fossils that Thoroddsen had donated to the museum in Stockholm. When Nathorst died in 1921, he had not finished his work on the Arctic floras. Apparently, he gave priority to the Palaeozoic and Mesozoic floras and intended to subsequently work on the Cainozoic floras. Nevertheless, Nathorst's illustrators had already prepared a

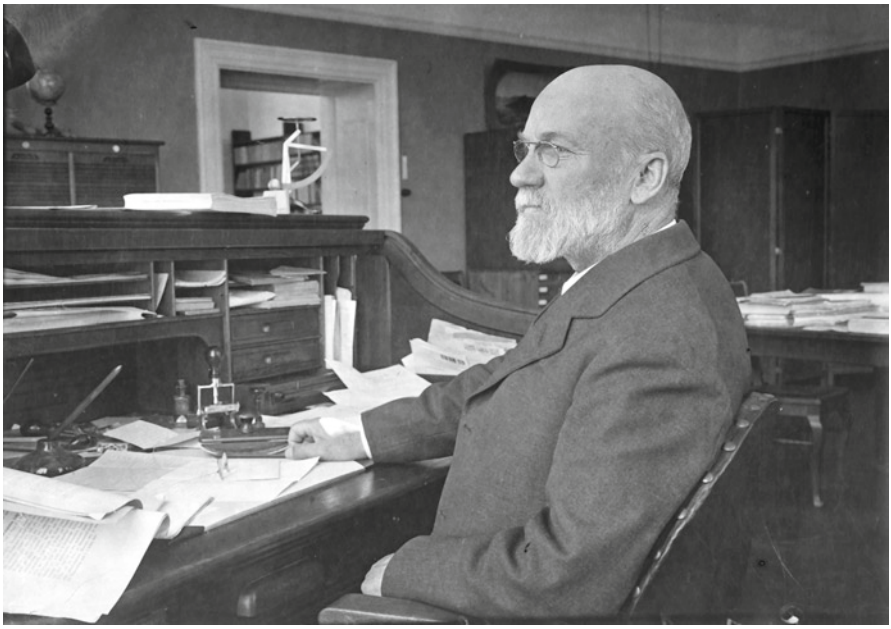


**Fig. 14.1** The Swedish palaeobotanists Alfred Gabriel Nathorst (1850–1921). Photograph taken by T. G. Halle, 1916

first set of drawings and plates of Palaeogene fossils from Spitsbergen collected during expeditions in 1882 by Nathorst and in 1890 by A. E. Nordenskiöld (cf. Kvaček et al. 1994; Kvaček and Manum 1997; Manum 1997). These plates were already printed before Nathorst's death (37 plates published and commented in 1997 by Kvaček & Manum). A second set of 38 sheets with hundreds of drawings of fossils from Spitsbergen, prepared later by Thérèse Ekblom, have never been reproduced nor have they been published. The same is true for a set of 46 sheets showing Neogene plant fossils from Iceland (Plates 14.1–14.46) prepared by Carl Hedelin and Thérèse Ekblom (under her maiden name Jansson).

## 14.3 Short Biographical Sketches of Carl Hedelin and Thérèse Ekblom

Between the years 1885 and 1921 Nathorst employed two graphic artists, Carl Hedelin and Thérèse Ekblom, to prepare illustrations for his publications.

Carl Hedelin (1861–1894) was employed in 1885 and remained Nathorst's illustrator until his tragic and much too early death in 1894. Hedelin's story is for the most part a sad one. He was born in Borås, southwestern Sweden. His family was poor and Hedelin's father died when he was still a boy, leaving him to take over as man and sole provider of the household at the age of ten. Hedelin worked in a carpenter's workshop and it was there that his artistic talents were discovered by his employers.

**Soeben erschienen:**

# ZUR FOSSILEN FLORA DER POLARLÄNDER

von

Prof. Dr. A. G. NATHORST.

**Erster Theil. — Erste Lieferung:**

## ZUR PALÄOZOISCHEN FLORA DER ARKTISCHEN ZONE,

enthaltend

die auf Spitzbergen, auf der Bären-Insel und auf Novaja Zemlja von den schwedischen Expeditionen entdeckten paläozoischen Pflanzen.

*Mit 16 Tafeln. Preis: M. 15,00.*

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Für die Beurtheilung der früheren klimatischen Verhältnisse der Erde sind wohl keine Fossilien von grösserer Bedeutung, als die fossilen Pflanzen der Polarländer. Unsere jetzige Kenntniss derselben verdanken wir zum grössten Theil HEER's Untersuchungen, deren Resultate in seinem berühmten Werke »Flora fossilis arctica» niedergelegt sind. Schon vor Vollendung desselben war von der schwedischen Polarexpedition 1882 neues Material zusammengebracht, jedoch wollte HEER dessen Bearbeitung nicht mehr übernehmen, sondern wünschte, dass sie von A. G. NATHORST ausgeführt werden möchte.

In der That ist Professor Dr NATHORST, welcher bereits zahlreiche wichtige Arbeiten über die fossilen Floren Schwedens und Japans veröffentlicht und selbst einen grossen Theil des neuen Materials während seines Aufenthaltes in Spitzbergen und Grönland zusammengebracht hat, hierzu besonders berufen.

Die jetzt vorliegende Abhandlung »Zur paläozoischen Flora der arktischen Zone» bildet die erste Lieferung eines grösseren Werkes ***''Zur fossilen Flora der Polarländer,''*** dessen Herausgabe als Fortsetzung der »Flora fossilis arctica» von Professor NATHORST beabsichtigt wird. Die zweite Lieferung, mit 4—6 Tafeln, soll die mesozoische Flora Spitzbergens enthalten, während die dritte, mit etwa 40 Tafeln, die Tertiärflora desselben Landes, von welcher jetzt ausgezeichnete Sammlungen vorliegen, darstellen wird.

Für die übrigen Theile des Werkes liegen neue Materialien aus Island, Grönland und Kamtschatka vor.

**Fig. 14.2** Note about the release of the first part of Nathorst's *Zur Fossilen Flora der Polarländer* in the Swedish journal *Geologiska Föreningens i Stockholm Förhandlingar* (1894). It is mentioned that Tertiary plants from Iceland were planned to be part of subsequent volumes of this work (see last two lines of announcement)

The manager of the workshop was so impressed by Hedelin's drawing skills that he arranged a collection to finance the young man's education. At the age of 16, Hedelin started his first year in a manual labour school in Stockholm, and later he was accepted into the Royal Academy of Fine Arts. Hedelin's skills soon gained him a reputation as a very promising young artist. During his studies he supported himself using his drawing skills, making various illustrations for journals and magazines. In 1885, Hedelin was hired by Nathorst and became an illustrator at the Swedish Museum of Natural History. For nine years he made illustrations for Nathorst's publications. In spring 1894, at the age of 33, he could afford a visit to Paris. The trip to Paris was a dream long in the making for him – an opportunity to see the capital of arts at that time; Paris was the place of rendezvous for many famous painters. Shortly after arriving in Paris, Hedelin was arrested, accused of attempted theft in a Paris gallery. Hedelin's trial was brief and unfair. His French was limited, he did not respond to questioning, he offered no defence, and he received no help from Swedish authorities in France. Consequently, he was sentenced to one year's imprisonment. After only a few weeks in prison he hanged himself (Roosval and Lilja 1957).

Relatively few palaeobotanical illustrations by Hedelin were published before his death (cf. Nathorst 1890a, b, 1894). Most were published during the years following his death, between 1895 and 1910 (cf. Nathorst 1897, 1902a, 1906a, c, 1907b, 1908b, c, 1909b; also Florin 1920) and, therefore, these publications include illustrations both by Hedelin and his successor Thérèse Ekblom.

After Hedelin's untimely and tragic death in 1894, Thérèse Ekblom (1867–1941) became his successor in the same year and worked for Nathorst until he died in 1921. Thérèse Ekblom (born Jansson) was from a family of artists; her father and brother were scene painters at the Royal Swedish Opera. She married Axel Ekblom (1858–1914), who was also an illustrator at the Swedish Museum of Natural History having started work there in 1876. From the 1890s, the couple worked for different departments (botany, palaeobotany, vertebrate zoology, entomology) as well as for botanists at the botanical garden (*Hortus Bergianus*). In contrast to Hedelin, Ekblom was very much involved in the exhibitions and prepared numerous water colour paintings for this purpose (Beckman 1999). In the early twentieth century, Ekblom also made photographs for Nathorst, and for a period, Nathorst used pencil drawings and photographs prepared by Thérèse Ekblom simultaneously (Nathorst 1907a, c, 1908a, b, c, 1909a, b, 1911a, b, c).

## 14.4 The Iceland Drawings

The illustrations on the sheets, now published for the first time, were drawn by Hedelin (five sheets with fossils from Tröllatunga collected during the 1883 Greenland expedition) and Ekblom (the remaining sheets with fossils collected during various expeditions from 1883 to 1910, mostly by Thoroddsen but also by Bárðarson, see Chap. 2). Illustrations made by Hedelin and Ekblom look superficially very similar. However, there is a striking difference in how the two artists drew the texture of the sediment surrounding the plant imprints. Hedelin apparently used a rather soft pencil, holding it at a low angle and touching the paper with the

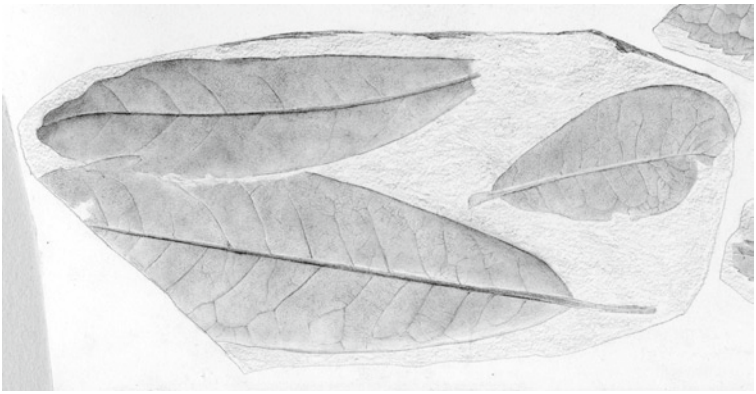


**Fig. 14.3** Pencil drawing by C. Hedelin showing his style of drawing the sedimentary rock surrounding the fossil

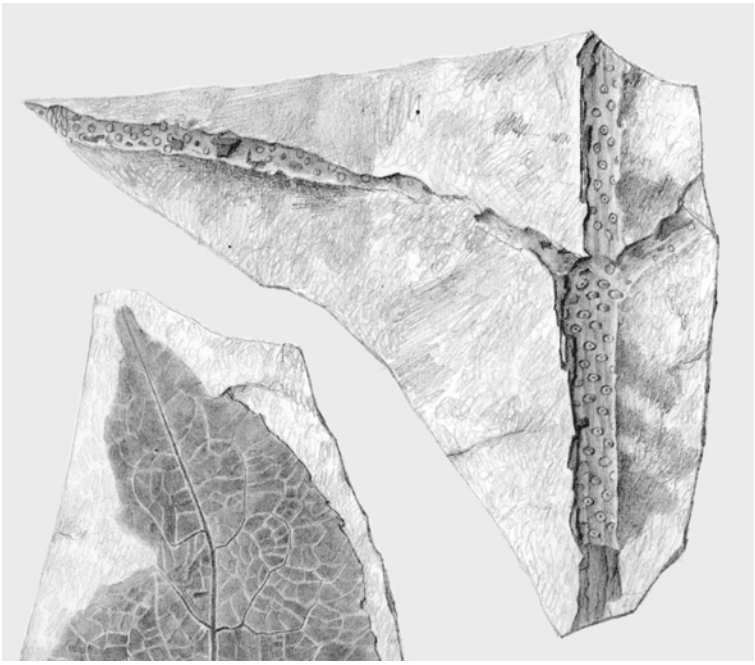


**Fig. 14.4** Pencil drawing by T. Ekblom showing her style of drawing the sedimentary rock surrounding the fossil

side of the pencil tip. The result was a homogeneous background and life-like image of the sediment (Fig. 14.3). In contrast, Ekblom probably used a harder pencil and did not attempt to show the sediment in a realistic way. She consistently used hatching consisting of short lines that regularly change direction or drew a swirled background (Fig. 14.4).

The sheets are large and the format is 14.6 x 28.8 cm. The original size of the sheets is too large for the format of this book (Fig. 14.5). In order to show the illustrations in

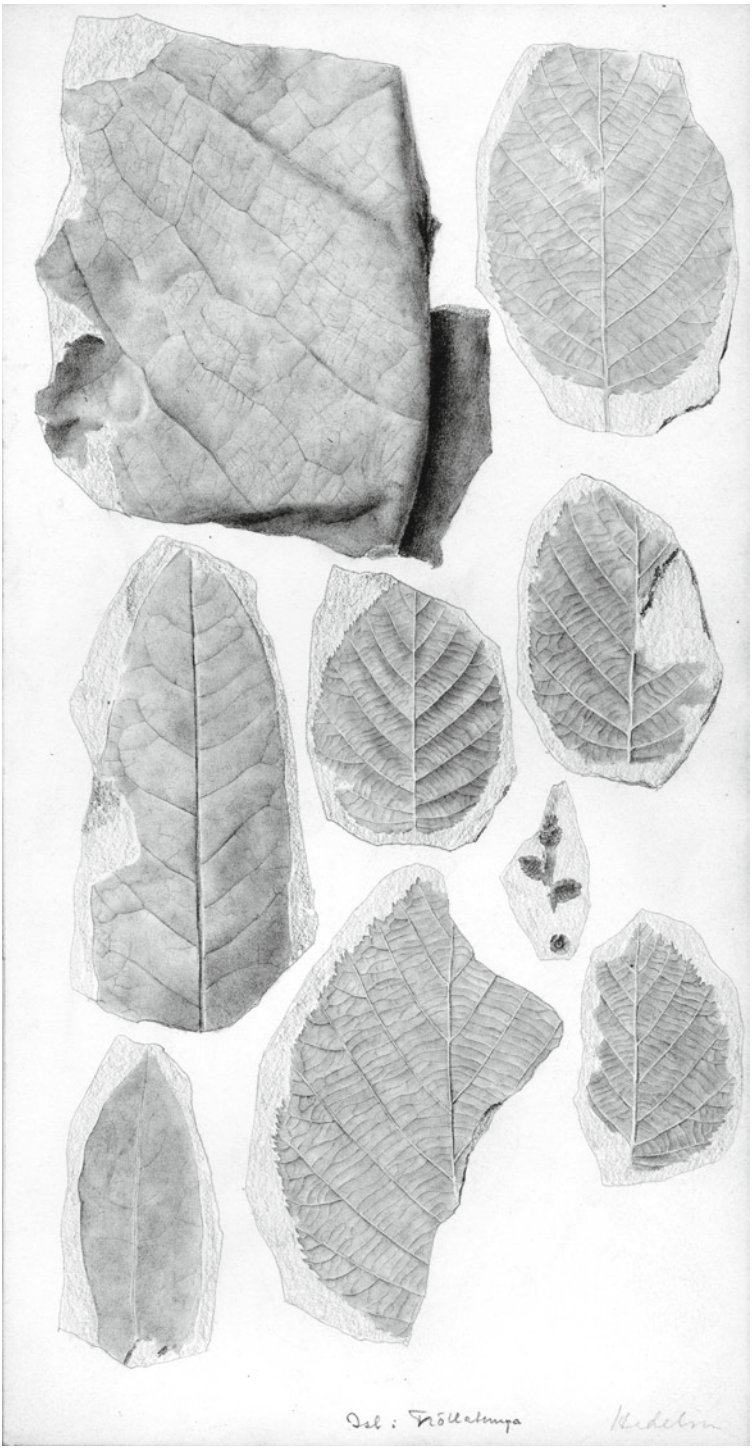



**Fig. 14.5** Original plate by C. Hedelin depicting fossils from Tröllatunga, Iceland. Plate has been re-sized to fit page

their original size, each illustration was scanned and rearranged, resulting in two smaller plates corresponding to one original. Some of the original sheets have been damaged after the death of Nathorst; some illustrations have been cut out. Most probably, illustrations that were cut out were planned to be used for publications (e.g., most illustrations of conifers were found as cut-outs in an envelope attached to the plates). One illustration of a maple leaf that is missing from the plates was published in an Icelandic journal by Bárðarson (1931).

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## Explanation of Plates

**Plate 14.1** (**a**) Fossils from Surtarbrandsgil, 12 Ma (Figs *1–7, 9, 12*), and Þrimilsdalur, 7–6 Ma (Figs *8, 10–11*). Drawings prepared by T. Ekblom (as Fröken Jansson). *1–2. Picea* sect. *Picea* sp., cones (S094008a, S094059). *3–6. Picea* sect. *Picea* sp., winged seeds (S094002, S116492, S094063-03, S094003) *7. Abies steenstrupiana* (Heer) Friedrich, winged seed (S094013). *8–12. Abies steenstrupiana*, cone scales (S106427, S094068-02, S106897, S094958, S094057) (**b**) Fossils from Tröllatunga, 10 Ma (Figs *1–4*), Surtarbrandsgil, 12 Ma (Figs *5, 7*), and Þrimilsdalur, 7–6 Ma (Fig *6*). Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Picea* sect. *Picea*, needles (S106781). *2–4.* (?) conifer leaves (S106644, S106616, S106569). *5. Tsuga* sp., leaf (S094004). *6. Abies steenstrupiana*, leaf (S094922). *7.* (?) female conifer cone (S094041)

**Plate 14.2** (**a**) Fossils from Surtarbrandsgil, 12 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Alnus cecropiifolia* (Ettingsh.) Berger, leaf (S094050-02). *2.* Rosaceae gen. et spec. indet., leaf (S094064-02). 3. *Betula islandica* Denk, Grímsson & Kvaček, leaf (S094029) (**b**) Fossils from Surtarbrandsgil, 12 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Corylus* sp., leaf (S094065-01). *2. Betula islandica*, leaf (S094064-01), *3. Corylus* sp., leaf (S094028-01)

**Plate 14.3** (**a**) Fossils from Surtarbrandsgil, 12 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1.* Betulaceae, leaf (S094981). *2. Ulmus* cf. *pyramidalis* Goepp., leaf (S093964-01). *3.* Rosaceae gen. et spec. indet. type A, leaf (S087422-02) (**b**) Fossils from Surtarbrandsgil, 12 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Laurophyllum* sp., leaf (S094035-01). *2.* Betulaceae, leaf (S094037). *3. Alnus cecropiifolia*, leaf (S094036)

**Plate 14.4** (**a**) Fossils from Surtarbrandsgil, 12 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1–2. Acer* sp., leaf (S094034-02, S093998). *3. Betula islandica*, leaf (S094058) (**b**) Fossils from Surtarbrandsgil, 12 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Alnus cecropiifolia*, leaf (S093938-02). *2. Alnus gaudinii* (Heer) Knobloch & Kvaček, leaf (S094033). *3. Betula islandica*, leaf (S087422-01)

**Plate 14.5** (**a**) Fossils from Surtarbrandsgil, 12 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1–2. Acer crenatifolium* Ettingsh. subsp. *islandicum* (Heer) Denk, Grímsson & Kvaček, leaf (S094006-01, S094007) (**b**) Fossils from Surtarbrandsgil, 12 Ma. Drawings prepared by

T. Ekblom (as Fröken Jansson). *1. Acer crenatifolium* subsp. *islandicum*, leaf (S093995-01). *2. Alnus gaudinii*, leaf (S093745-01). *3.* Betulaceae, leaf (S094985)

**Plate 14.6** (**a**) Fossils from Surtarbrandsgil, 12 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1.* Rosaceae gen et. spec. indet., leaf (S094030). *2. Acer crenatifolium* subsp. *islandicum*, leaf (S094000). *3. Alnus cecropiifolia*, leaf (S093939). *4. Acer crenatifolium* subsp. *islandicum*, leaf (S094028-02) (**b**) Fossils from Surtarbrandsgil, 12 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1.* Betulaceae, leaf (S094060-01). *2. Abies steenstrupiana*, seed (S094032-01). *3.* Rosaceae gen et. spec. indet., leaf (S094019-01). *4–5. Alnus cecropiifolia*, leaf (S094032-02, S094039). *6. Alnus gaudinii*, leaf (S094019-02). *7. Betula islandica*, leaf (S094060-02)

**Plate 14.7** (**a**) Fossils from Surtarbrandsgil, 12 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Magnolia* sp., leaf (S094054). *2. Abies* sp., axis (S094024) *3. Dicotylophyllum* sp. 1, leaf (S094020) (**b**) Fossils from Surtarbrandsgil, 12 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Magnolia* sp., leaf (S094018). *2. Liriodendron procaccinii* Unger, fruit (S094043). *3. Magnolia* sp., leaf (S094068-01)

**Plate 14.8** Fossils from Surtarbrandsgil, 12 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Alnus gaudinii*, leaf (S093951). *2. Dicotylophyllum* sp. 2 (‘*Lonicera*’), leaf (S093952)

**Plate 14.9** (**a**) Fossils from Surtarbrandsgil, 12 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Salix gruberi* Denk, Grímsson & Kvaček, leaf (S093954-01). *2. Dicotylophyllum* sp.1, leaf (S093977-01). *3. Alnus gaudinii*, leaf (S094984). *4. Smilax* sp., leaf (S093953-01). *5. Rosaseae* gen. et spec. indet., leaf (S094012). *6. Alnus gaudinii*, leaf (S093936-02). 7. *Alnus cecropiifolia*, leaf (S093947) (**b**) Fossils from Surtarbrandsgil, 12 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1.* Rosaceae gen. et spec. indet., leaf (S093943). *2. Ulmus* cf. *pyramidalis*, leaf (S094005). *3. Alnus cecropiifolia*, leaf (S093950). *4. Alnus* sp., leaf (S093945). *5. Acer crenatifolium* subsp. *islandicum*, samara (S093935-02). *6. Betula islandica*, fruit scales (S093963). *7. Betula islandica*, leaf (S093997*). 8. Dicotylophyllum* sp. 2 (‘*Lonicera’*), leaf (S093937). *9. Dicotylophyllum* sp. 1, leaf (S093936-01)

**Plate 14.10** (**a**) Fossils from Surtarbrandsgil, 12 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Sassafras ferrettianum* Massalongo, leaf (S093993). *2. Abies steenstrupiana*, cone scale (S094049-02). *3.* cf. Rosaceae, leaf (S094063-02). *4. Betula islandica*, leaf (S094031). *5.* Rosaceae gen. et spec. indet. type A, leaf (S094017) (**b**) Fossils from Surtarbrandsgil, 12 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1.* Rosaceae gen. et spec. indet. type B, leaf (S094044). *3. Betula islandica*, leaf (S094015). *4. Alnus* sp., leaf (S904016). *5. Alnus cecropiifolia*, leaf (S094983). *6. Acer* sp., leaf (S094047). *7. Acer crenatifolium* subsp. *islandicum*, leaf (S094049-01)

**Plate 14.11** (**a**) Fossils from Surtarbrandsgil, 12 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Comptonia hesperia* Berry, leaf (S094066). *2. Sassafras ferrettianum*, leaf (S094989) *3.* Unidentified, leaf (S094001) *4.* Unidentified, leaf (S094063-01) (**b**) Fossils from Surtarbrandsgil, 12 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Sassafras* cf. *ferrettinaum*, leaf (S094021). *2. Dicotylophyllum* sp. 1, leaf (S094046). *3. Magnolia* sp., leaf (S093996) *4. Dicotylophyllum* sp. 3 (‘Neolitsea’), leaf (S094061). *5. Dicotylophyllum* sp. 1, leaf (S094067)

**Plate 14.12** (**a**) Fossils from Surtarbrandsgil, 12 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1–2. Acer crenatifolium* subsp. *islandicum*, leaf (S094010-01, S093958) (**b**) Fossils from Surtarbrandsgil, 12 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Alnus cecropiifolia*, leaf (S093942). *2. Acer crenatifolium* subsp. *islandicum*, leaf (S093815). *3. Alnus cecropiifolia*, leaf (S093946). *4. Betula islandica*, leaf (S093838-01)

**Plate 14.13** (**a**) Fossils from Surtarbrandsgil, 12 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Alnus cecropiifolia*, leaf (S094987). *2. Acer crenatifolium* subsp. *islandicum*, leaf (S094023) (**b**) Fossils from Surtarbrandsgil, 12 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Acer crenatifolium* subsp. *islandicum*, leaf (S094011)

**Plate 14.14** (**a**) Fossils from Surtarbrandsgil, 12 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Acer crenatifolium* subsp. *islandicum*, leaf (S093960); 80% original size (**b**) Fossils from Surtarbrandsgil, 12 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1–2. Acer crenatifolium* subsp. *islandicum*, leaf (S093940, S094025-01). *3. Sassafras ferrettianum*, leaf (S093962)

**Plate 14.15** (**a**) Fossils from Fífudalur, 7–6 Ma (Figs 1–2) and Gautshamar, 10 Ma (Figs 3–5). Drawings prepared by T. Ekblom (as Fröken Jansson). *1–2. Salix gruberi*, leaf (S094093). *3.* Betulaceae, leaf (S094202). *4. Acer crenatifolium* subsp. *islandicum*, leaf (S094288-02). *5. Alnus cecropiifolia*, leaf (S116413) (**b**) Fossils from Gautshamar, 10 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1–3. Alnus cecropiifolia*, leaf (S094288-01, S094273-02, S094360)

**Plate 14.16** (**a**) Fossils from Gautshamar, 10 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Alnus cecropiifolia*, leaf (S094144). *2. Acer crenatifolium*, leaf (S094402). *3. Acer* sp., leaf (S094326) (**b**) Fossils from Gautshamar, 10 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1–4. Alnus cecropiifolia*, leaf (S094348, S094201, S116470, S094354-01). *5.* Betulaceae, young leaf (S094361). *6. Acer crenatifolium* subsp. *islandicum*, leaf (S094358). *7. Alnus* sp., leaf (S094275). *8–11. Alnus* cf. *kefersteinii* (Goepp.) Goepp., infructescence (S094232, S116494, S094218, S094079). *12.* Unidentified (S094236). *13.* cf. *Acer* sp., samara (S094200). *14–15.* cf. Betulaceae, catkin (S094205a, S094209). *16–17. Acer askelssonii* Friedrich & Símonarson, samara (S094212, S106898). *18. Acer* sp., samara (S094210). *19. Acer askelssonii* Friedrich & Símonarson, samara (S094212)

**Plate 14.17** (**a**) Fossils from Gautshamar, 10 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Acer* sp., leaf (S094273-01). *2.* Betulaceae, leaf (S094408). *3.* Betulaceae, leaf (S094401). *4. Acer crenatifolium* subsp. *islandicum*, leaf (S094314) (**b**) Fossils from Gautshamar, 10 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1.* cf. *Alnus cecropiifolia*, leaf (S094339). *2.* cf. *Pterocarya*, leaf (S094407). *3. Alnus cecropiifolia*, leaf (S094312). *4.* Betulaceae, leaf (S094322). *5–6. Acer crenatifolium* subsp. *islandicum*, samara (S094168, S094394). *7–8. Equisetum* sp., sheath of whorled leaves (S094412-01, S094413)

**Plate 14.18** (**a**) Fossils from Gautshamar, 10 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1–4. Acer crenatifolium* subsp. *islandicum*, leaf (S116471, S094416, S094396, S094418) (**b**) Fossils from Gautshamar, 10 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Acer askelssonii*, leaf (S094385a) *2–5. Acer crenatifolium* subsp. *islandicum*, leaf (S094345, S094344, S094343, S094423)

**Plate 14.19** (**a**) Fossils from Gautshamar, 10 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1–2. Equisetum* sp., rhizome (S116472, S094588). *3–4.* Cyperaceae, leaf (S094552, S094542-01). *5–6. Osmunda parschlugiana* (Unger) Andreánszky, leaflet (S106895, S094733a) (**b**) Fossils from Gautshamar, 10 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Acer crenatifolium* subsp. *islandicum*, leaf (S094574-01)

**Plate 14.20** (**a**) Fossils from Húsavíkurkleif, 10 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Acer crenatifolium* subsp. *islandicum*, leaf (S116473). *2. Acer askelssonii*, leaf (S094536). *3. Salix gruberi*, leaf (S116474). *4.* Cyperaceae, leaf (S094580). *5. Acer crenatifolium*

subsp. *islandicum*, leaf (S094756) (**b**) Fossils from Húsavíkurkleif, 10 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1.* cf. *Corylus* sp., leaf (S094750-01) *2.* aff. *Pterocarya/Cyclocarya*, leaflet (S094752) *3.* Betulaceae, leaf (S094745a) *4.* cf. *Acer* sp., leaf (S094516) *5.* Pteridophyta gen. et spec. indet. 1, pinna (S094732). *6.* cf. Juglandaceae, leaf (S094587). *7. Salix gruberi*, leaf (S094628)

**Plate 14.21** (**a**) Fossils from Húsavíkurkleif, 10 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Salix gruberi*, leaf (S094633). *2.* Unidentified (S094746). *3–6. Salix gruberi*, leaf (S094631, S094626, S094606, S094630). *7–8.* Betulaceae, leaf (S094632, S094545) (**b**) Fossils from Húsavíkurkleif, 10 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Alnus cecropiifolia*, leaf (S094556-01). *2. Acer crenatifolium* subsp. *islandicum*, samara (S094592). *3.* Betulaceae, leaf (S094739). *4. Acer crenatifolium* subsp. *islandicum*, samara (S116475). *5–7.* Betulaceae, leaf (S094738, S094754, S094751)

**Plate 14.22** (**a**) Fossils from Húsavíkurkleif (Fig. 1) and Tröllatunga (Figs 2–15), 10 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Acer* sp., leaf (S116476). *2–3. Rhododendron* sp., bud scales (S106499a, S106526-01). *4. Osmunda parschlugiana*, pinna (S106764). *5.* cf. *Arctostaphylos* sp. (deciduous), leaf (S106768). *6. Vaccinium* sp. (evergreen type), leaf (S106769). *7. Osmunda parschlugiana*, frond (S106766). *8–9. Vaccinium* sp. (evergreen type), leaf (S106759, S106767). *10. Picea* sp., seed (S116495). *11. Osmunda parschlugiana*, pinna (S106537). *12. Picea* sect. *Picea*, male cone (S106517a). *13. Vaccinium* sp. (evergreen type), leaf (S116496) (**b**) Fossils from Tröllatunga, 10 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Acer* sp., leaf (S106614-01). *2–3.* aff. *Pterocarya/Cyclocarya*, leaflet (S106534, S106743-01). *4. Osmunda parschlugiana*, pinna (S106564). *5. Osmunda parschlugiana*, small pinna (S106532). *6.* aff. *Pterocarya/Cyclocarya*, leaflet (S106515). *7. Alnus kefersteinii*, infructescence (S106556). *8–9.* aff. *Pterocarya/Cyclocarya*, leaflet (S106545-02, S106545-01)

**Plate 14.23** (**a**) Fossils from Tröllatunga, 10 Ma. Drawings prepared by C. Hedelin. *1–2. Alnus cecropiifolia*, leaf (S106736, S106726). *3.* aff. *Pterocarya/Cyclocarya*, leaflet (S116477) (**b**) Fossils from Tröllatunga, 10 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson); Fig. 1 perhaps by C. Hedelin. *1.* Betulaceae, leaf (S116478). *2. Vaccinium* sp. (evergreen type), leaf (S106690). *3. Alnus cecropiifolia*, leaf (S106604). *4–5. Vaccinium* sp. (evergreen type), leaf (S106624-01, S106660). *6. Rhododendron* aff. *ponticum*, leaf (S106567). *7. Vaccinium* sp. (evergreen type), leaf (S106658). *8.* cf. Arct*ostaphylos* sp. (deciduous), leaf (S106621). *9.* cf. aff. *Pterocarya/Cyclocarya*, leaflet (S106755). *10. Larix* sp., branch with spur shoots (S106536)

**Plate 14.24** (**a**) Fossils from Tröllatunga, 10 Ma. Drawings prepared by C. Hedelin. *1. Nuphar* sp., leaf (S106522). *2. Alnus cecropiifolia*, leaf (S106776-02). *3. Larix* sp., branch with spur shoots (S106776-01). *4–5. Alnus cecropiifolia*, leaf (S106700, S106776-01) (**b**) Fossils from Tröllatunga, 10 Ma. Drawings prepared by C. Hedelin. *1. Rhododendron* aff. *ponticum*, leaf (S106705). *2. Alnus cecropiifolia*, leaf (106737). *3. Rhododendron* aff. *ponticum*, leaf (S106702). *4. Alnus cecropiifolia*, leaf (106721)

**Plate 14.25** Fossils from Tröllatunga, 10 Ma (Fig. 1–2, and 4–8) and Þrimilsdalur, 7–6 Ma (Fig. 3). Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Alnus cecropiifolia*, leaf (S116480). *2.* aff. *Pterocarya/Cyclocarya*, leaflet (S106481). *3. Acer askelssonii*, samara (S094953-01). *4–5. Smilax* sp., leaf (S106749, S106746). *6. Rhododendron* sp., bud scale (S106704). *7. Alnus kefersteinii*, infructescence (S106754). *8.* aff. *Pterocarya/Cyclocarya*, leaflet (S106631)

**Plate 14.26** (**a**) Fossils from Tröllatunga (10 Ma). Drawings prepared by C. Hedelin. *1. Rhododendron* aff. *ponticum*, leaf (S087459). *2.* aff. *Pterocarya/Cyclocarya*, leaflet (S106722a-01). *3.* Rosaceae gen. et spec. indet. type A, leaf (S106524-01). *4. Dicotylophyllum*

sp. 4, leaf (S106673) (**b**) Fossils from Tröllatunga (10 Ma). Drawings prepared by C. Hedelin. *1*. Acer *crenatifolium* subsp. *islandicum*, leaf (S106720). *2–3. Alnus cecropiifolia*, leaf (S106718-01, 106639a). *4. Acer crenatifolium* subsp. *islandicum*, leaf (S106718-02)

**Plate 14.27** (**a**) Fossils from Tröllatunga (10 Ma). Drawings prepared by C. Hedelin. *1. Rhododendron* aff. *ponticum*, leaf (S106760-01). *2. Acer crenatifolium* subsp. *islandicum*, samara (S106715-01). *3. Alnus cecropiifolia*, leaf (S106677-01). *4.* cf. *Acer* sp., samara fragment (S106677-02). *5–7.* Unidentified (S106760-02, S116482, S106760-03) (**b**) Fossils from Tröllatunga (10 Ma). Drawings prepared by C. Hedelin. *1–3*. aff. *Pterocarya/Cyclocarya*, leaflet (S106722b-01, S106630-01, S116483)

**Plate 14.28** Fossil from Tröllatunga (10 Ma). Drawing prepared by C. Hedelin. *1*. aff. *Pterocarya/Cyclocarya*, leaflet (S106525-01)

**Plate 14.29** (**a**) Fossils from Tröllatunga (10 Ma). Drawings prepared by C. Hedelin. *1. Acer crenatifolium* subsp. *islandicum*, leaf (S106725). *2. Nuphar* sp., leaf (S106711) (**b**) Fossils from Tröllatunga (10 Ma). Drawings prepared by C. Hedelin. *1. Nuphar* sp., leaf (S106502). *2. Alnus cecropiifolia*, leaf (S106735). *3.* aff. *Pterocarya/Cyclocarya*, leaflet (S106733-01)

**Plate 14.30** (**a**) Fossils from Tröllatunga, 10 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Rhododendron* aff. *ponticum*, leaf (S106740-01). *2.* aff. *Pterocarya/Cyclocarya*, leaflet (S106765). *3. Alnus cecropiifolia*, leaf (S106708-01). *4–5. Acer crenatifolium* subsp. *islandicum*, samara (S106710, S106580-02) *6. Alnus cecropiifolia*, leaf (S106773-01) (**b**) Fossils from Tröllatunga, 10 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1–3. Alnus cercopiifolia*, leaf (S106508-01, S106713, S106717-01). *4–5. Acer crenatifolium* subsp. *islandicum*, samara (S106717-02, S106693)

**Plate 14.31** Fossils from Tröllatunga, 10 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1–6. Acer crenatifolium* subsp. *islandicum*, leaf (S106778, S106730, S106745-01, S106535b, S106744, S116484)

**Plate 14.32** (**a**) Fossils from Tröllatunga, 10 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1–4. Acer crenatifolium* subsp. *islandicum*, leaf (S106739, S106703, S116485, S106728-01) (**b**) Fossils from Tröllatunga, 10 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1–5. Acer crenatifolium* subsp. *islandicum*, leaf (S106674, S116486, S106708-02, S106774, S106578)

**Plate 14.33** (**a**) Fossils from Seljá, 12 Ma. Drawings prepared by T. Ekblom (as Fröken Jansson). *1–2. Phragmites* sp., rhizome (S106795, S106790). *3. Alnus cecropiifolia*, leaf (S106801a). *4–6. Salix gruberi*, leaf (S106804, S106809, S106785-01). *7.* Unidentified, leaf (S106785-03) (**b**) Fossils from Seljá, 12 Ma (Figs 1–3, 5–6, 8) and from Margrétarfell, 10 Ma (Figs 4, 7). Drawings prepared by T. Ekblom (as Fröken Jansson). *1–3. Salix gruberi*, leaf (S106783, S106782, S106785-02). *4.* Unidentified, leaf (S094761) *.5. Phragmites* sp., rhizome (S106796). *6.* Unidentified, axis (S106811). *7. Osmunda parschlugiana*, pinna (S094758). *8.* Unidentified, leaf (S106786a)

**Plate 14.34** Fossil from Hrútagil (9–8 Ma). Drawing prepared by T. Ekblom (as Fröken Jansson). *1. Acer* sp., leaf (S105952-01)

**Plate 14.35** Fossils from Hrútagil (9–8 Ma). Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Acer askelssonii*, leaf (S094787). *2.* cf. Betulaceae, leaf (S094771-01), 90% original size

**Plate 14.36** (**a**) Fossil from Hrútagil (9–8 Ma). Drawing prepared by T. Ekblom (as Fröken Jansson). *1. Fagus gussonii* Massalongo, leaf (S106893) (**b**) Fossils from Hrútagil (9–8 Ma).

Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Acer crenatifolium* subsp. *islandicum*, leaf (S105946-01). *2. Fagus gussonii*, leaf (S094799)

**Plate 14.37** (**a**) Fossil from Hrútagil (9–8 Ma). Drawing prepared by T. Ekblom (as Fröken Jansson). *1. Fagus gussonii*, leaf (S106894) (**b**) Fossils from Hrútagil (9–8 Ma). Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Fagus gussonii*, leaf (S094830). *2. Acer* sp., leaf (S094854). *3. Fagus gussonii*, leaf (S105954). *4. Betula* cf. *cristata*, leaf (S094805)

**Plate 14.38** (**a**) Fossils from Hrútagil (9–8 Ma). Drawings prepared by T. Ekblom (as Fröken Jansson). *1–2. Fagus gussonii*, leaf (S105953, S094801) (**b**) Fossils from Hrútagil (9–8 Ma). Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Fagus gussonii*, leaf (S105951). *2.* Unidentified, leaf (S094821)

**Plate 14.39** (**a**) Fossils from Hrútagil (9–8 Ma). Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Fagus gussonii*, leaf (S094816) *2.* Betulaceae, leaf (S094820) (**b**) Fossils from Hrútagil (9–8 Ma). Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Fagus gussonii*, leaf (S105955). *2. Betula* sp., leaf (S094798). *3. Fagus gussonii*, leaf (S094874)

**Plate 14.40** (**a**) Fossils from Fífudalur (7–6 Ma). Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Betula cristata* Lindquist emend. Denk, Grímsson & Kvaček, leaf (S094111). *2–4. Salix gruberi*, leaf (S094091, S094071, S094076). *5.* cf. *Tsuga* sp., leaf (S094080-02). *6. Salix gruberi*, leaf (S094086-01) (**b**) Fossils from Fífudalur (7–6 Ma). Drawings prepared by T. Ekblom (as Fröken Jansson). *1.* cf. *Crataegus* sp., leaf (S094081). *2–3. Betula cristata*, leaf (S094092, S094113). *4. Acer askelssonii*, samara (S116487). *5–6. Salix gruberi*, leaf (S094080-01, S094086-02). *7.* Betulaceae, leaf (S094070). *8. Salix* sp., capsule (S094075). *9. Picea* sp., seed (S094108)

**Plate 14.41** (**a**) Fossils from Fífudalur (7–6 Ma). Drawings prepared by T. Ekblom (as Fröken Jansson). *1–2. Salix gruberi*, leaf (S094107, S094088). *3. Acer askelssonii*, samara (S094084-01). *4. Alnus* vel *Betula*, leaf (S094097) (**b**) Fossils from Fífudalur (7–6 Ma). Drawings prepared by T. Ekblom (as Fröken Jansson). *1–2.* cf. *Betula cristata*, leaf (S094094, S094118-01). *3. Salix gruberi*, leaf (S094118-02)

**Plate 14.42** (**a**) Fossils from Fífudalur (7–6 Ma). Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Betula cristata*, leaf (S094121). *2. Salix gruberi*, leaf (S094069). *3–5. Betula cristata*, leaf (S094085, S094090, S094109-01) (**b**) Fossils from Fífudalur (7–6 Ma). Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Betula cristata*, leaf (S094074). *2.* Betulaceae, leaf (S094141). *3–7. Salix gruberi*, leaf (S094110, S094083, S116488, S094099, S094101). *8. Acer* sp., samara (S094078-01). *9.* Pinaceae, leaf (S094078-02)

**Plate 14.43** (**a**) Fossils from Þrimilsdalur (7–6 Ma). Drawings prepared by T. Ekblom (as Fröken Jansson). *1–2. Acer askelssonii*, leaf (S106579-01) (**b**) Fossils from Þrimilsdalur (7–6 Ma). Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Betula cristata*, leaf (S094978). *2. Abies steentrupiana*, cone scale (S106579-02). *3. Betula cristata*, leaf (S094948). *4. Phragmites* sp., leaf (S094976). *5–7. Betula subnivalis* Lindquist, catkin scales (S094927, S106896-02, S094953-02)

**Plate 14.44** (**a**) Fossils from Þrimilsdalur (7–6 Ma). Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Acer askelssonii*, leaf (S094924). *2–6. Betula cristata*, leaf (S106420-01, S094903, S106896-01, S094894, S094896) (**b**) Fossils from Þrimilsdalur (7–6 Ma). Drawings prepared by T. Ekblom (as Fröken Jansson). *1.* cf, Salicaceae, axis, (S094961). *2–7. Betula cristata*, leaf (S094931, S116489, S094929, S094969, S094957, S094963). *8. Betula subnivalis*, catkin scale (S094899)

**Plate 14.45** (**a**) Fossils from Þrimilsdalur (7–6 Ma). Drawings prepared by T. Ekblom (as Fröken Jansson). *1. Betula cristata*, leaf (S116490). *2. Acer askelssonii*, leaf (S094946). *3.* Monocotyledon, leaf (S094897-01). *4–5. Betula cristata*, leaf (S094959, S094954-01) (**b**) Fossils from Þrimilsdalur (7–6 Ma). Drawings prepared by T. Ekblom (as Fröken Jansson). *1–5. Betula cristata*, leaf (S094933, S094897-03, S094914, S094916, S094960)

**Plate 14.46** (**a**) Fossils from Vindfell (7–6 Ma). Drawings prepared by T. Ekblom (as Fröken Jansson). *1–3. Salix gruberi*, leaf (S106886, S106879-01, S106836-01). *4.* Unidentified (S106854). *5. Picea* sp., seed (S106852). *6. Phragmites* sp., axis (S106883). *7. Tsuga* sp., leaf (106877). *8.* Pinaceae, seed (108859). *9. Salix gruberi*, leaf (106840) *10.* Unidentified, leaf (S106876) *11. Phragmites* sp., rhizome (S106885) *12. Phragmites* sp., axiz (S106835) (**b**) Fossil from Vindfell (7–6 Ma). Drawing prepared by T. Ekblom (as Fröken Jansson). *1. Phragmites* sp., axis (S116491)

# Plates

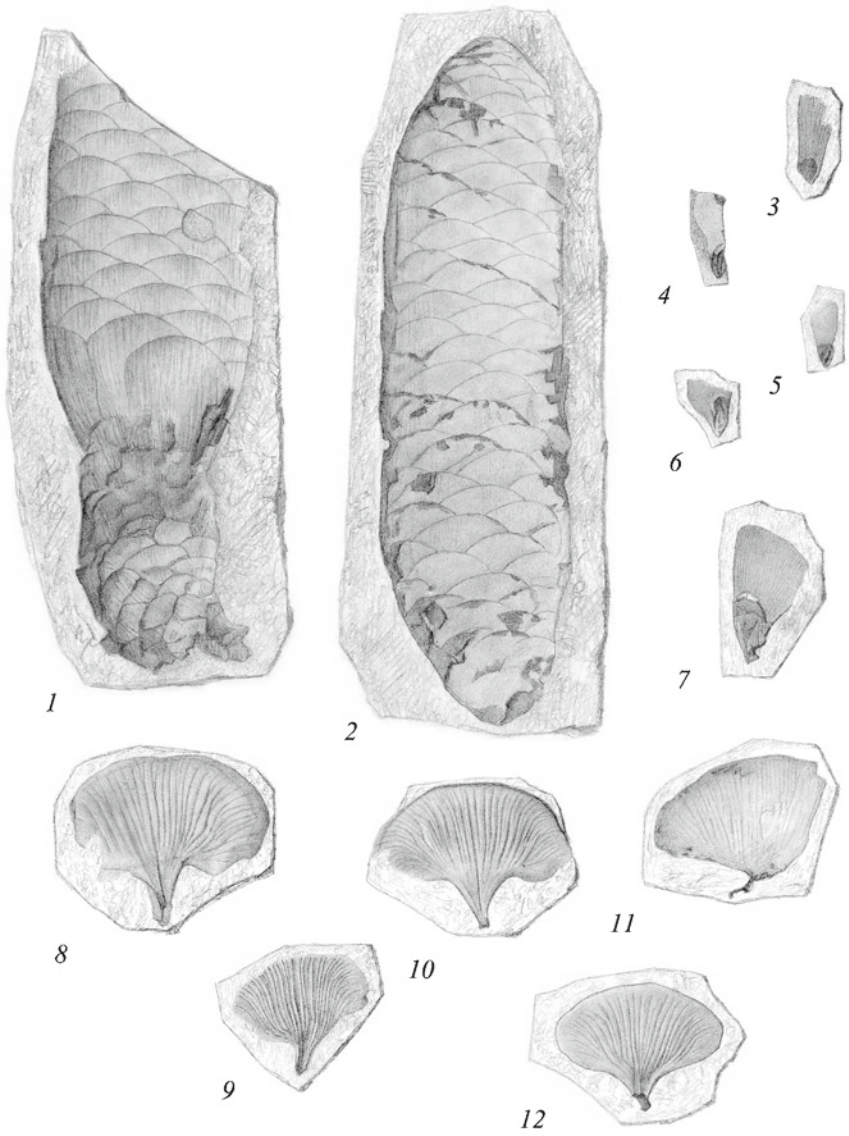



**Plate 14.1 (a)**

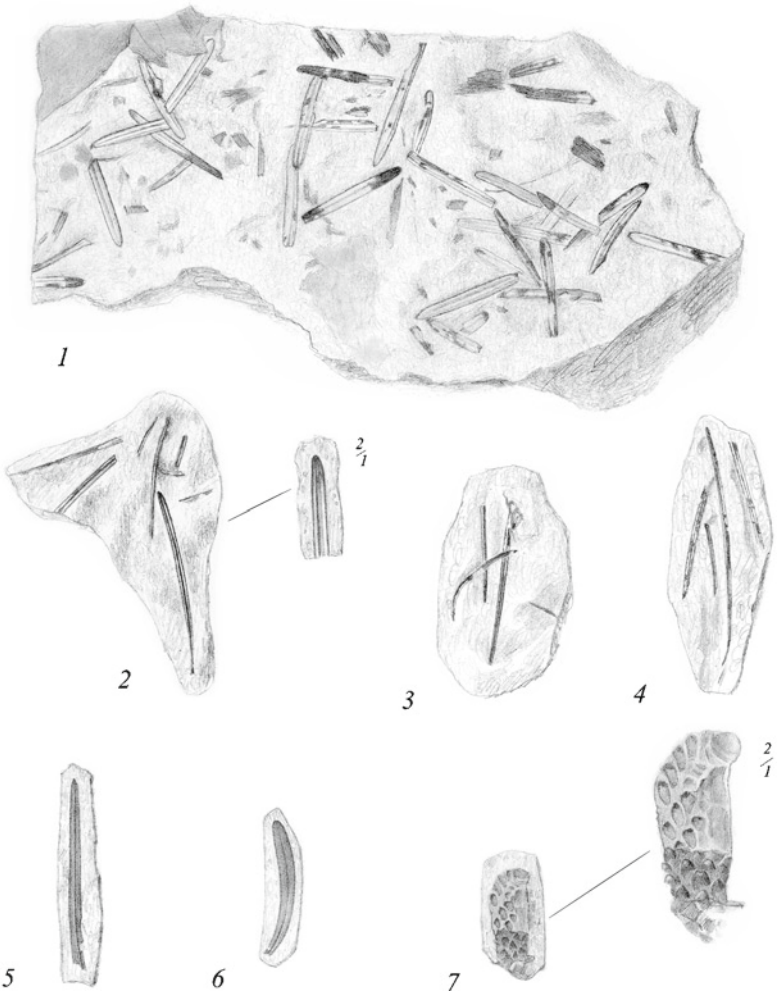



**Plate 14.1** (**b**)

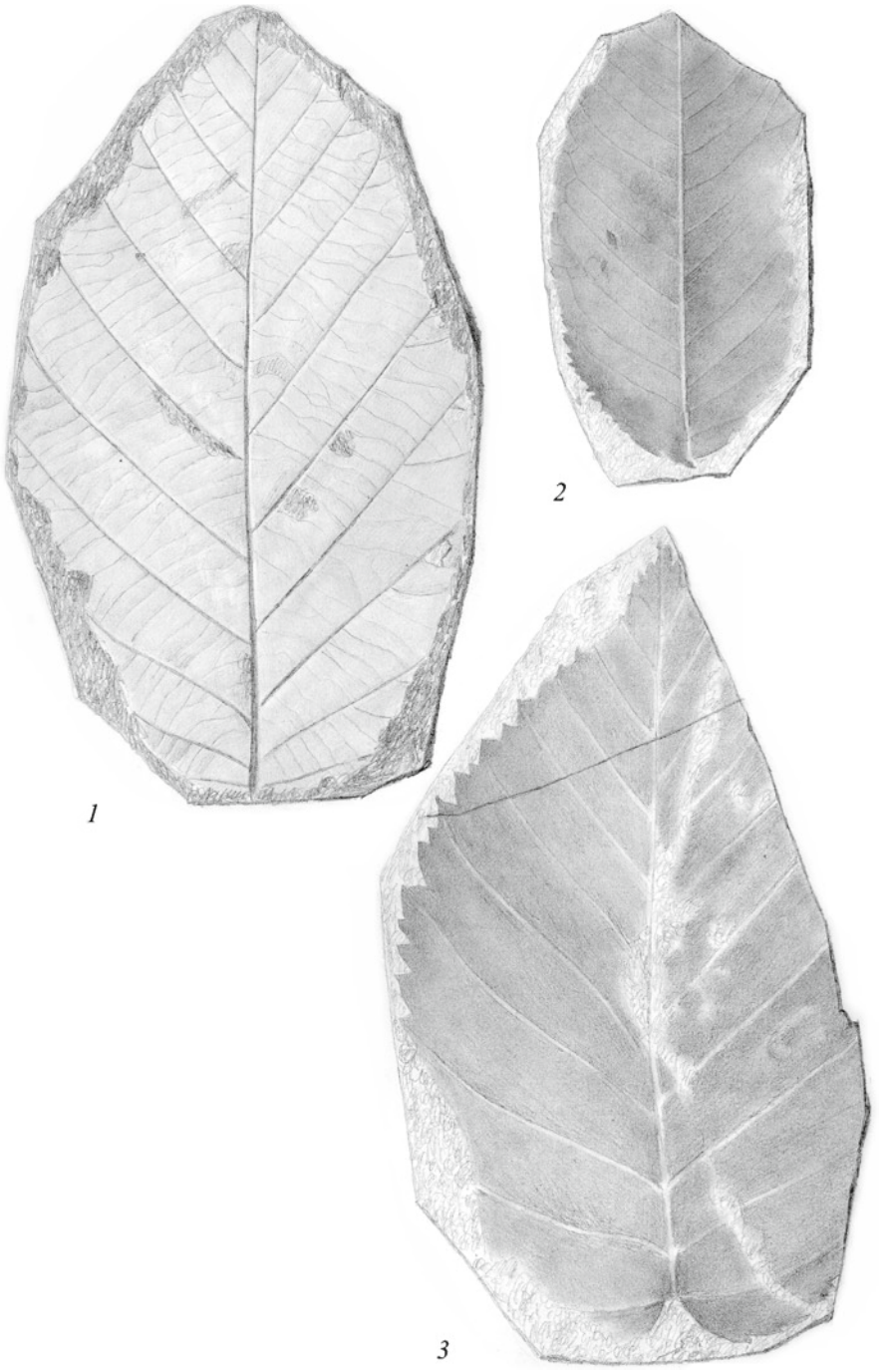



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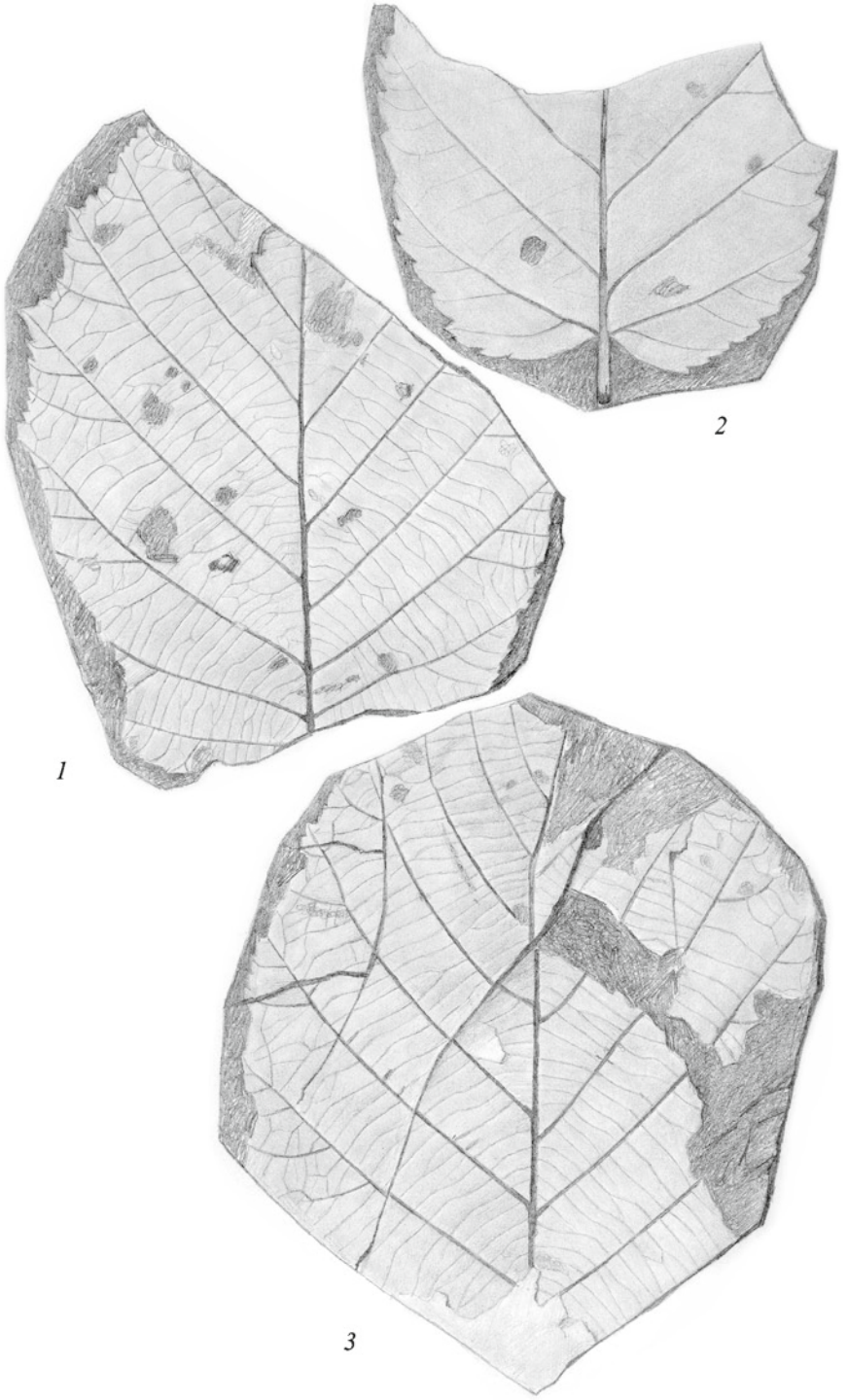



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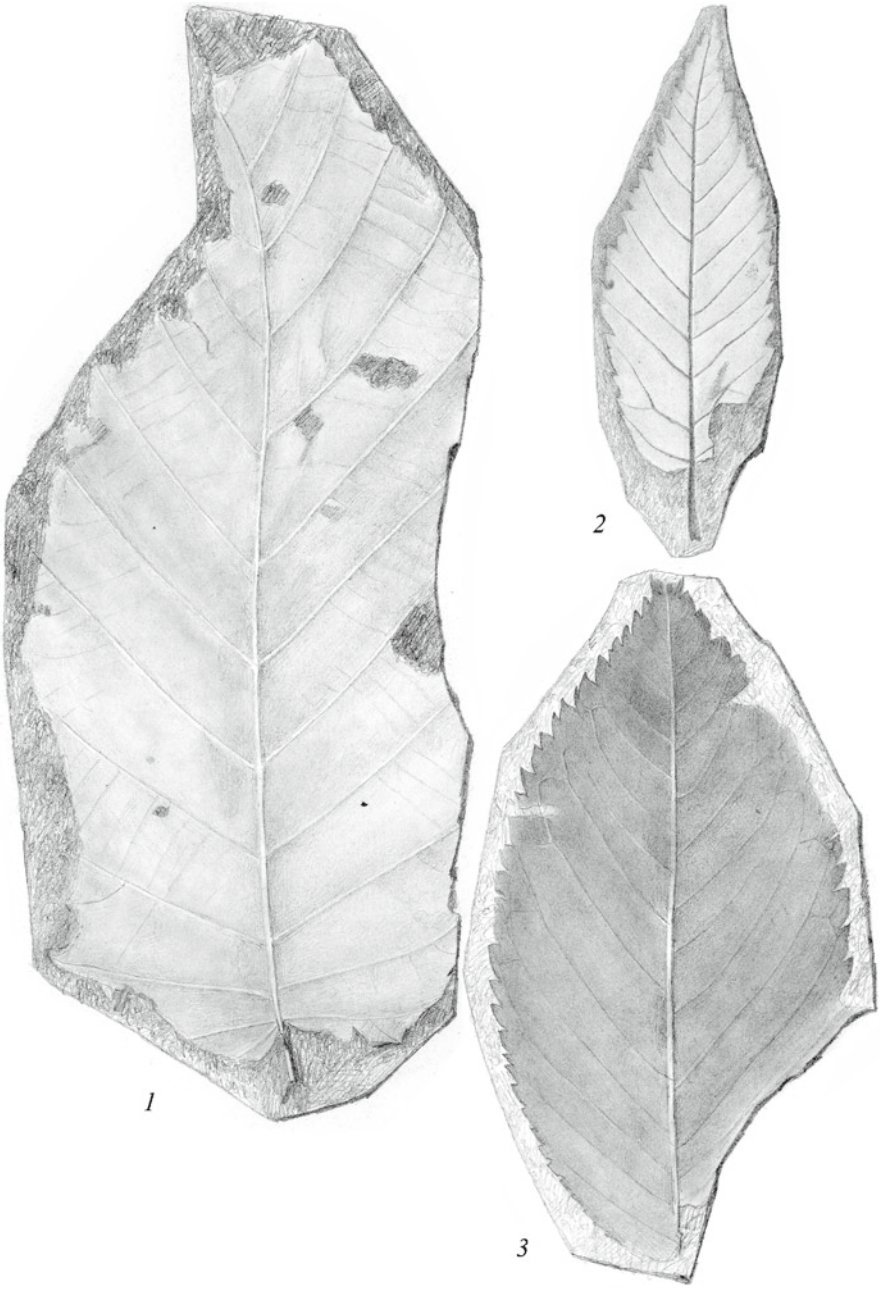



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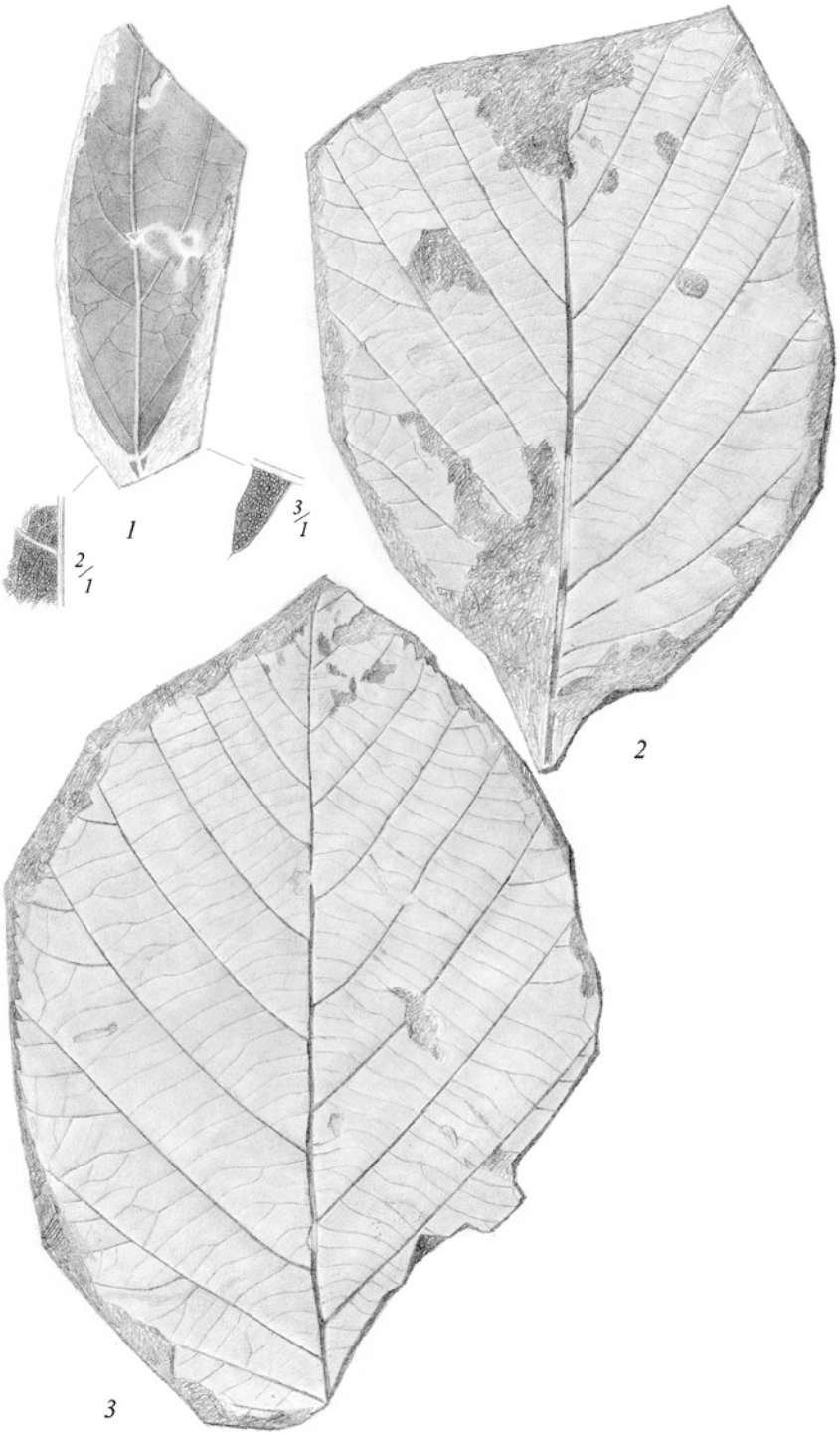



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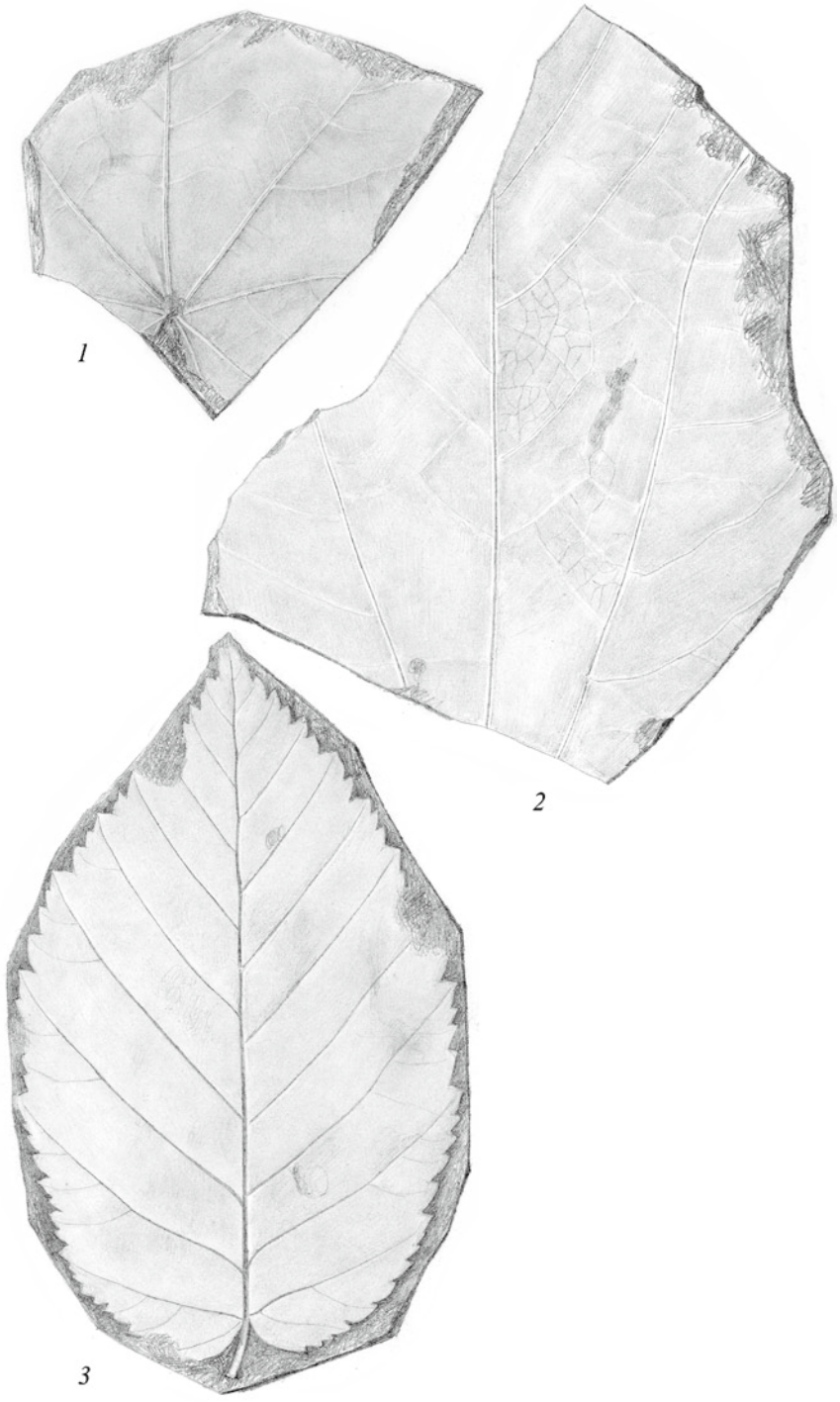



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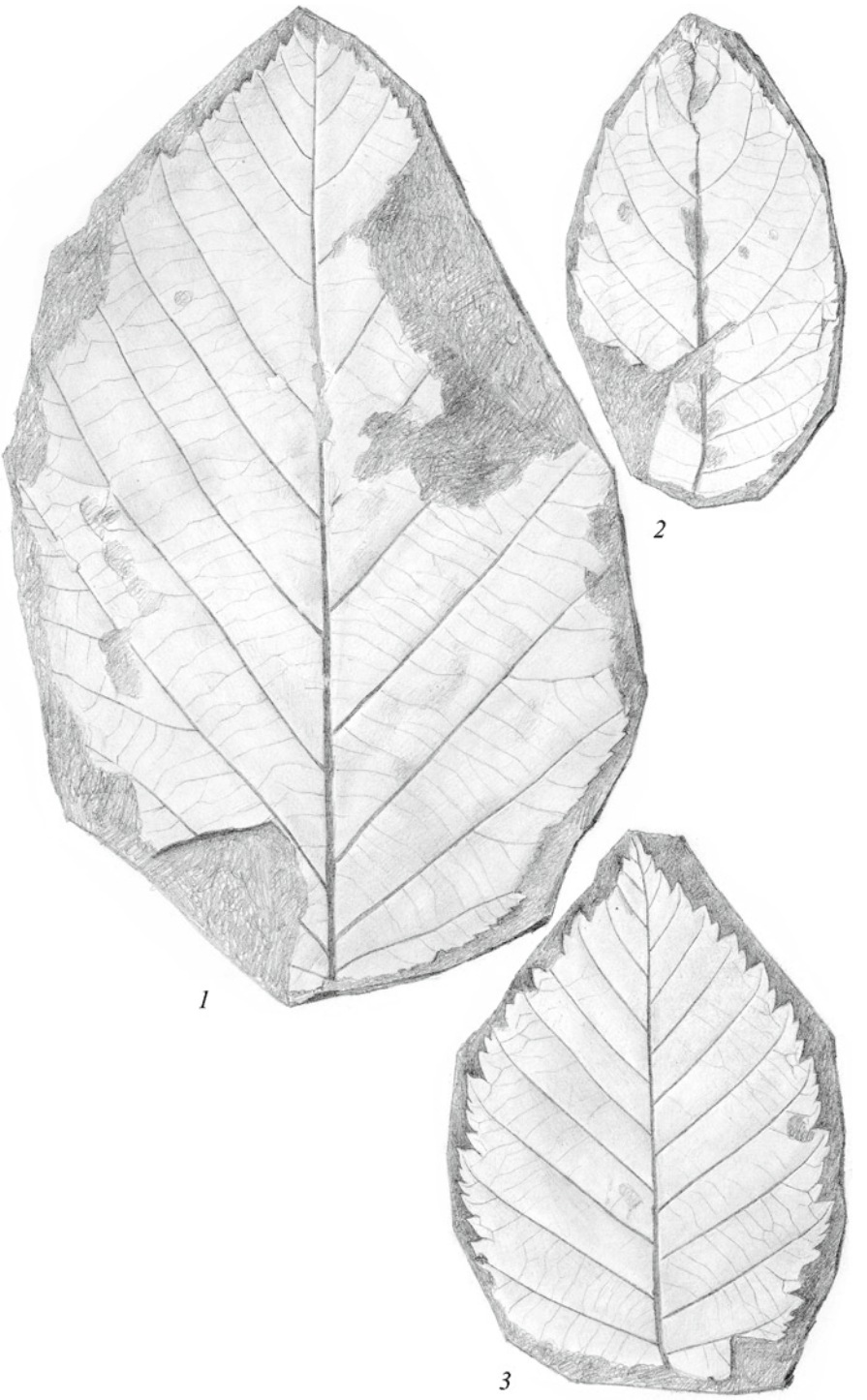



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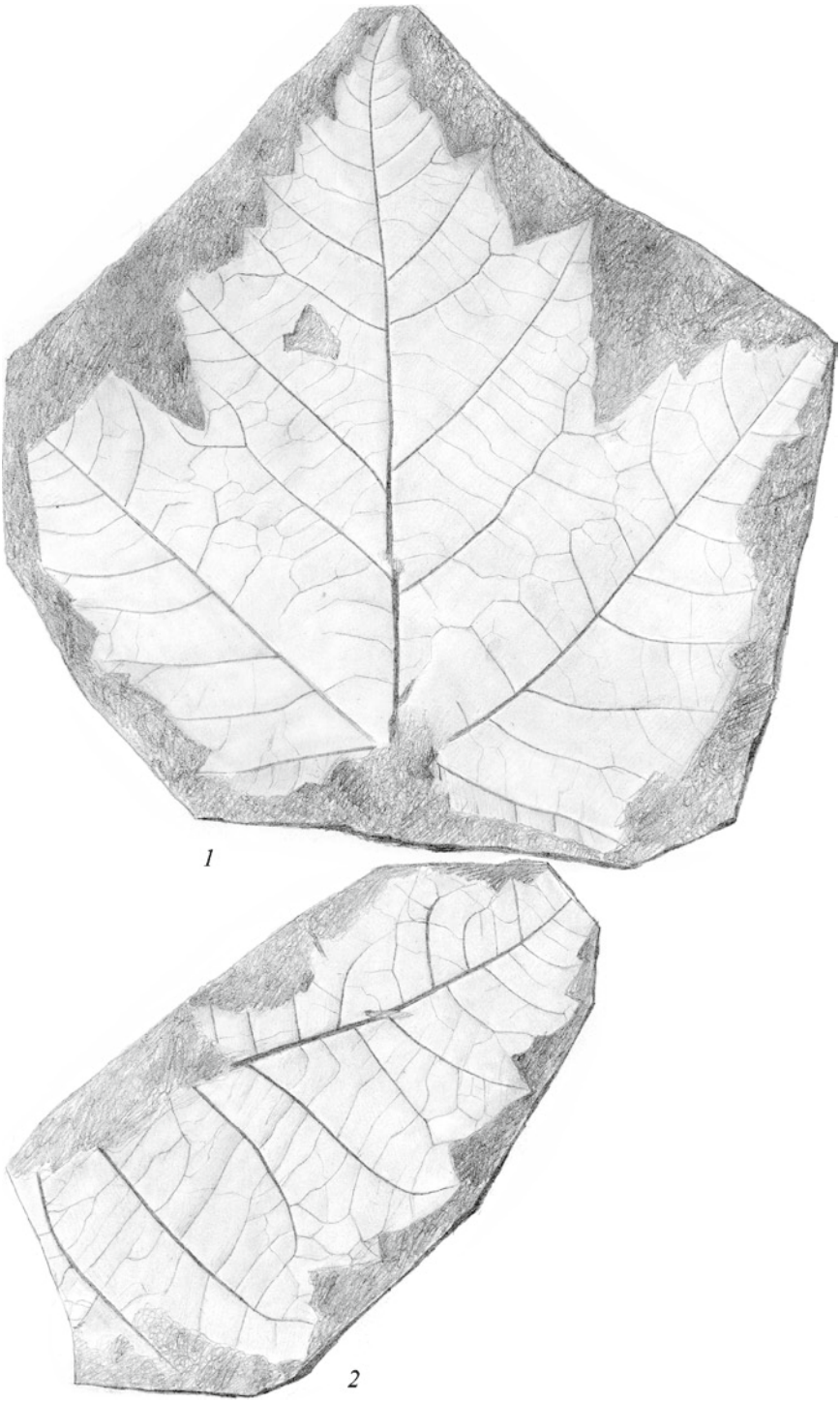



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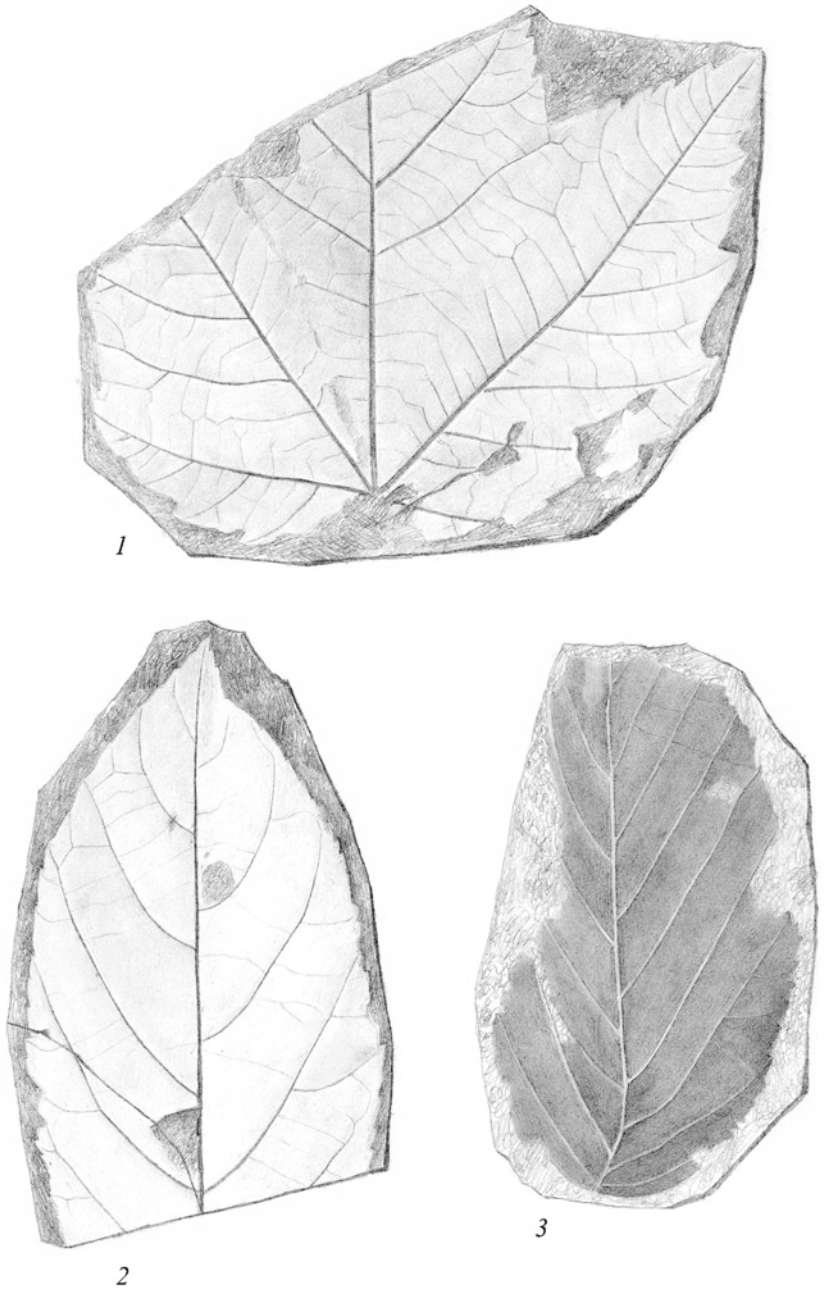



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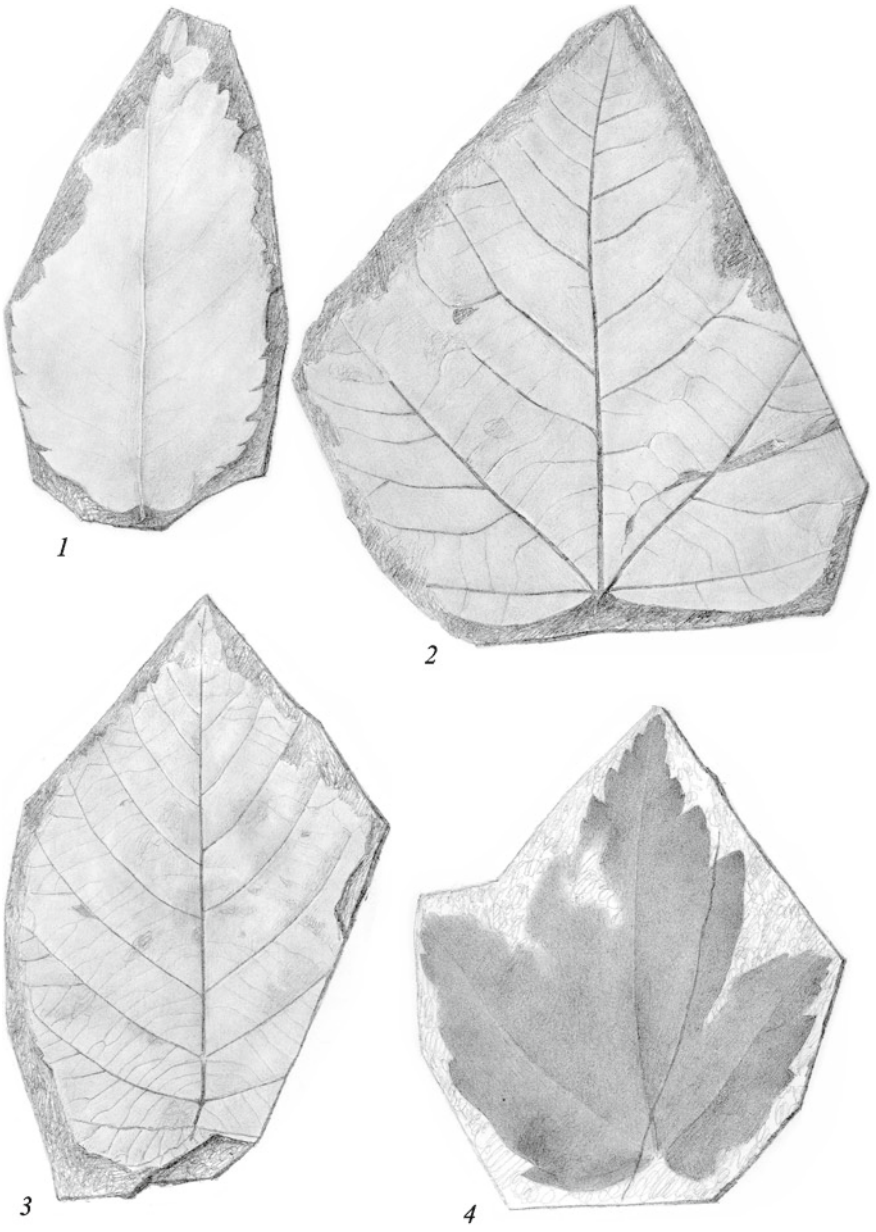



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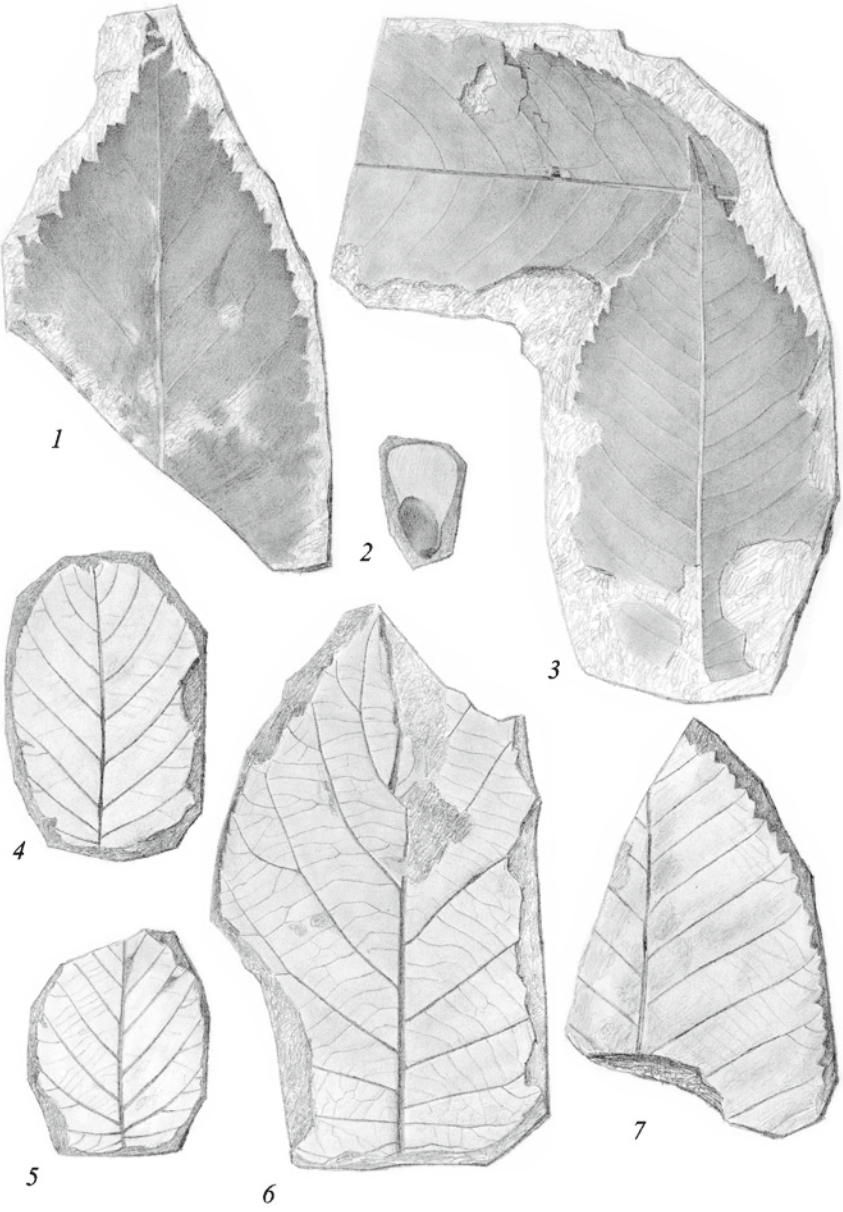



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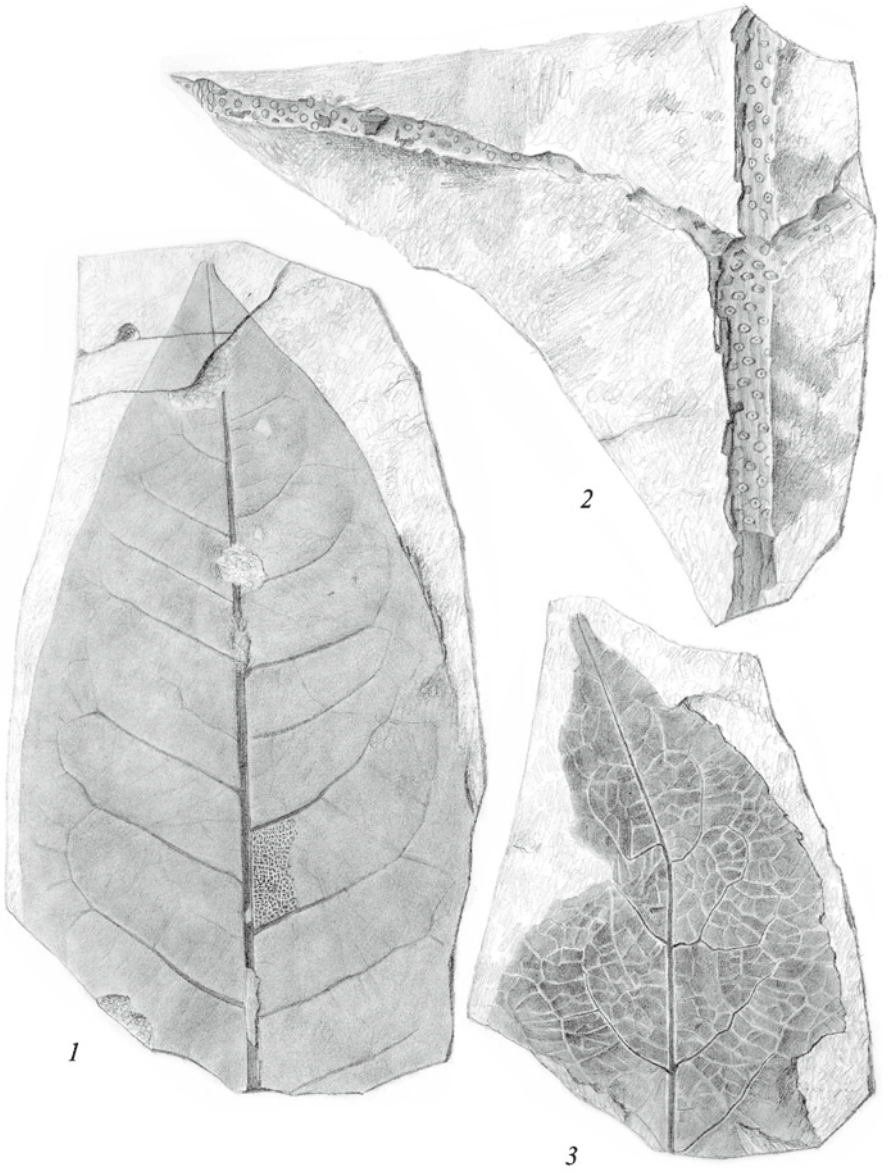



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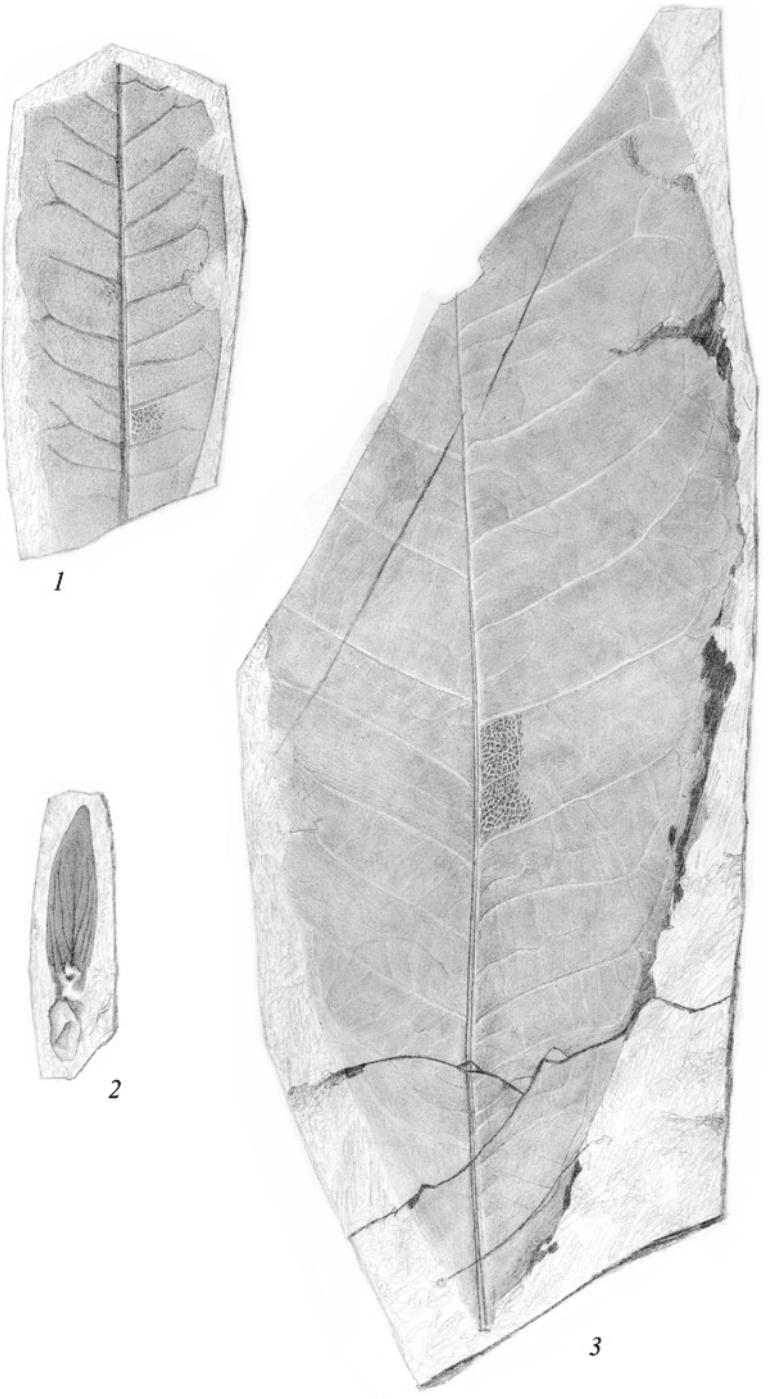



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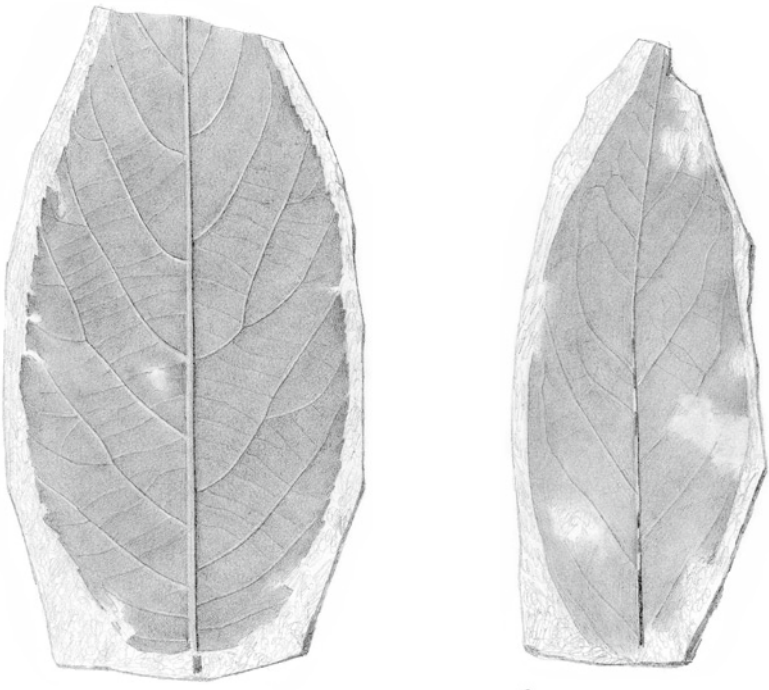



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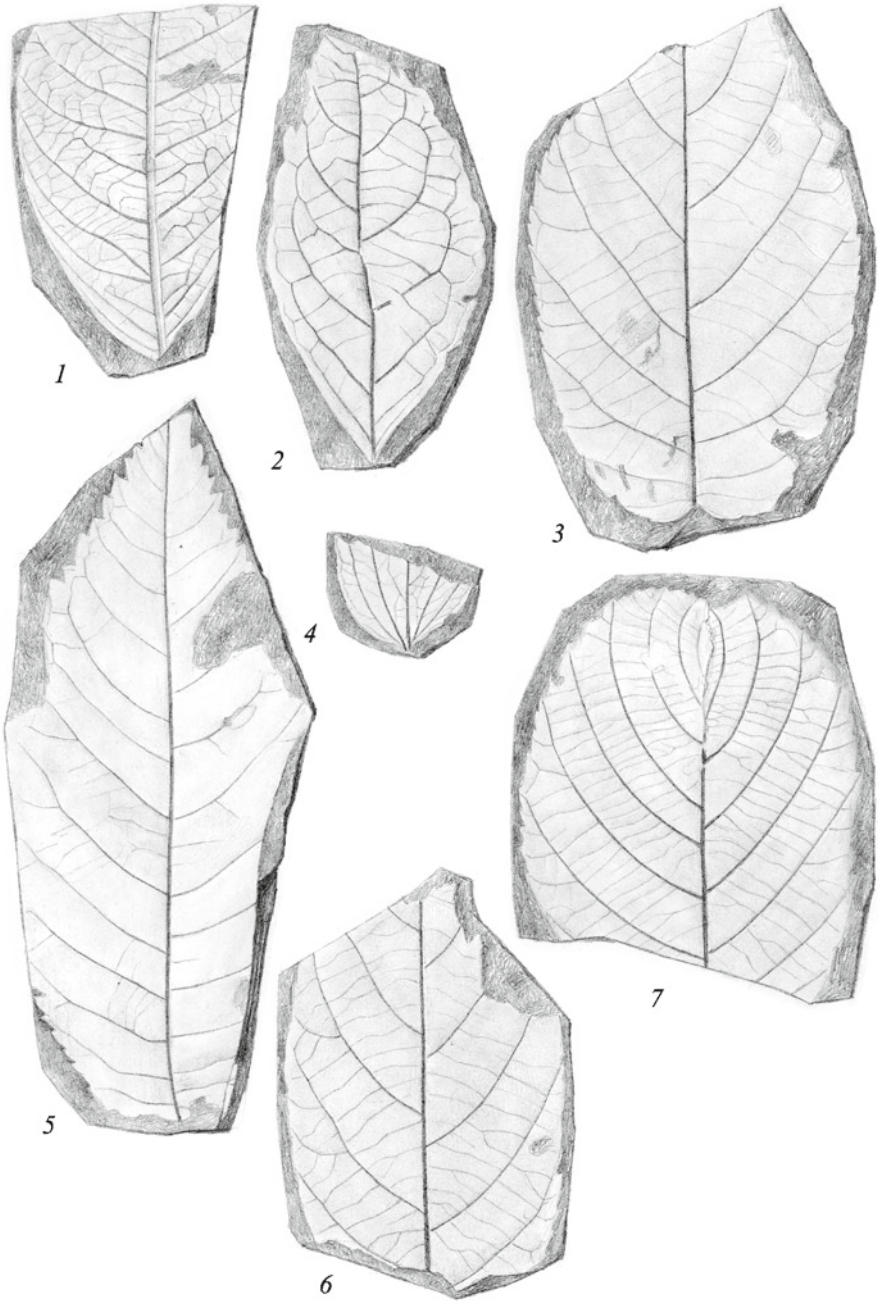



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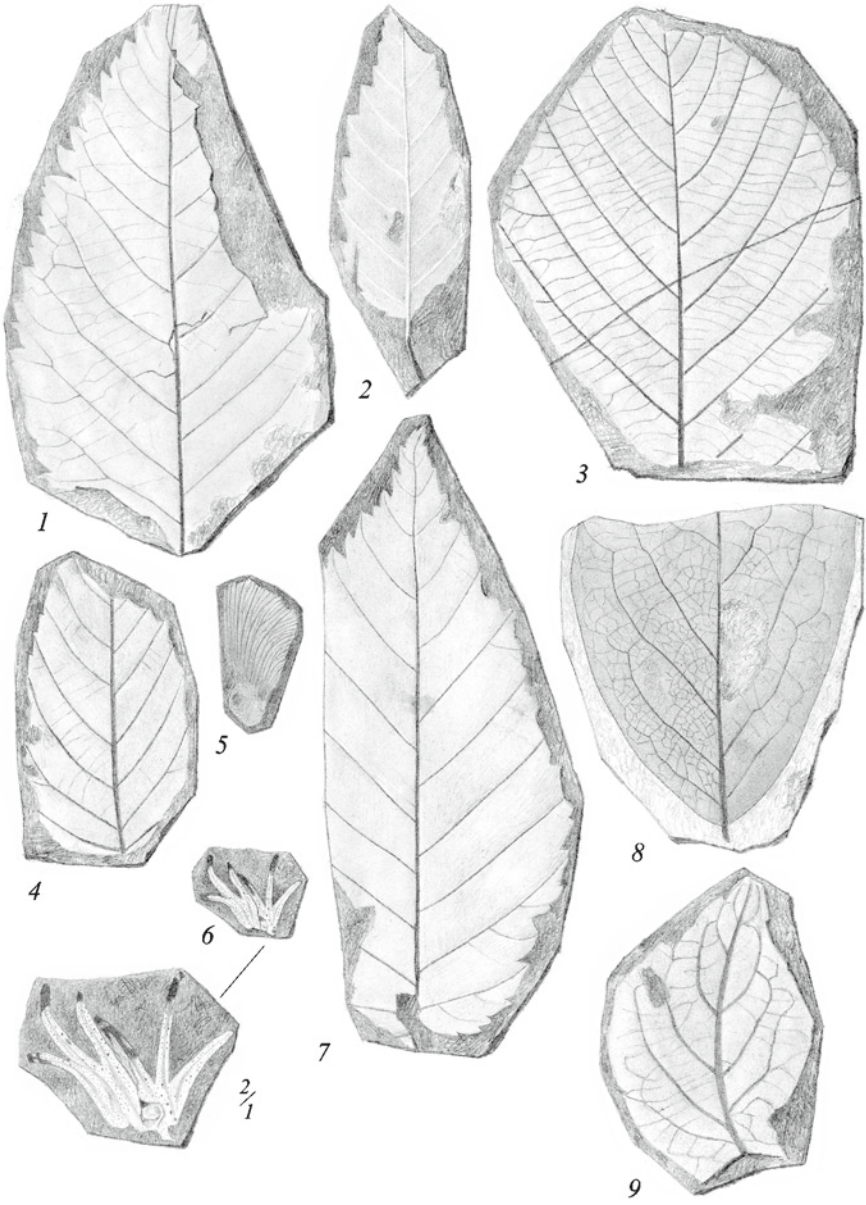



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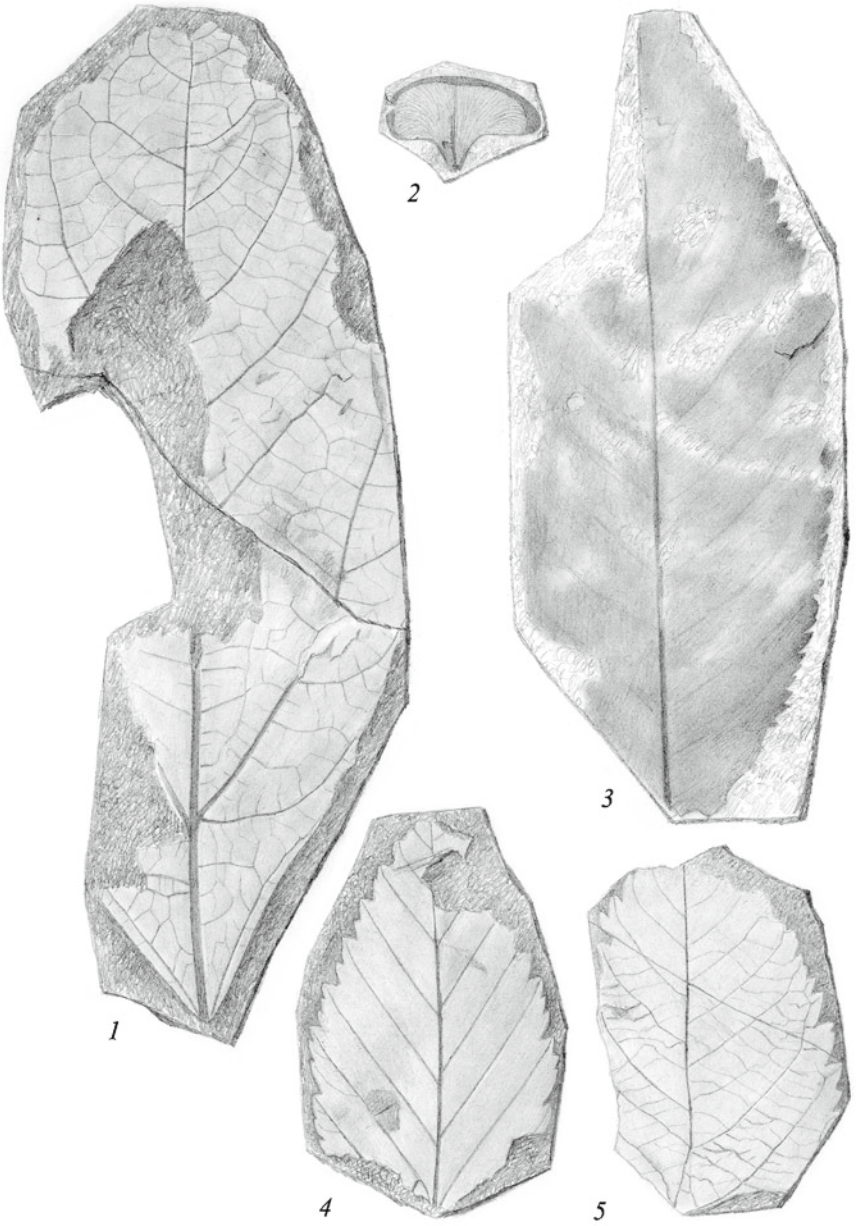



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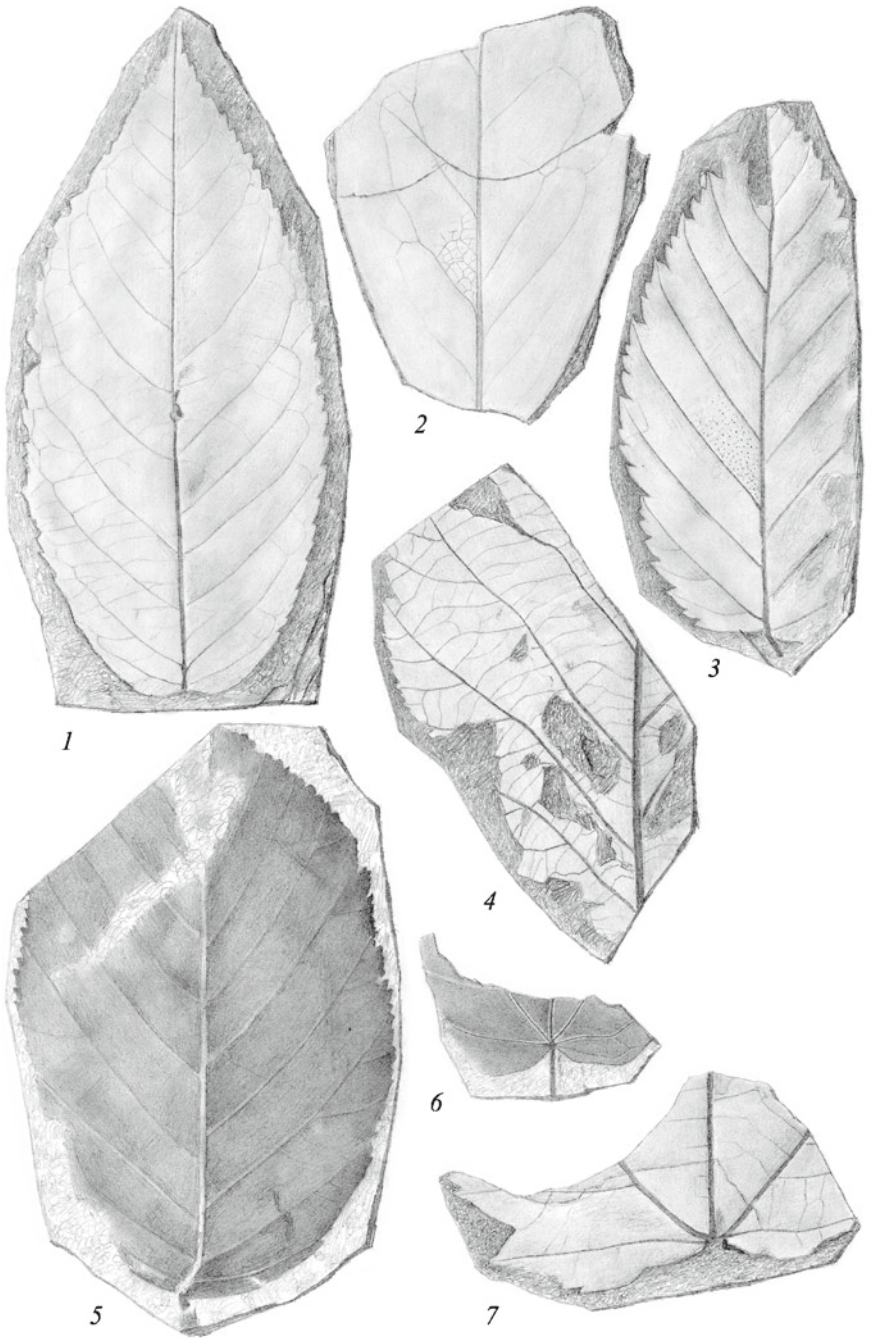



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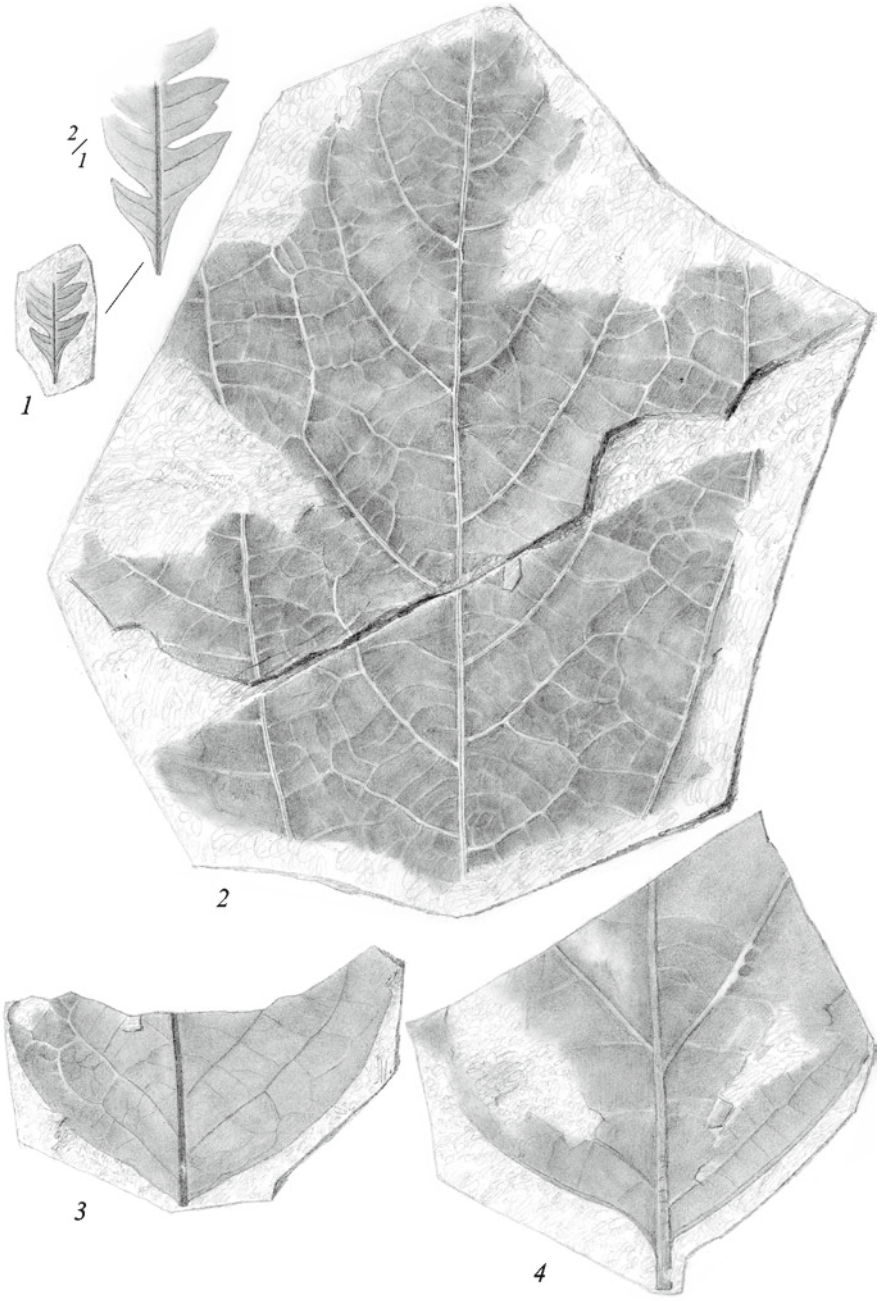



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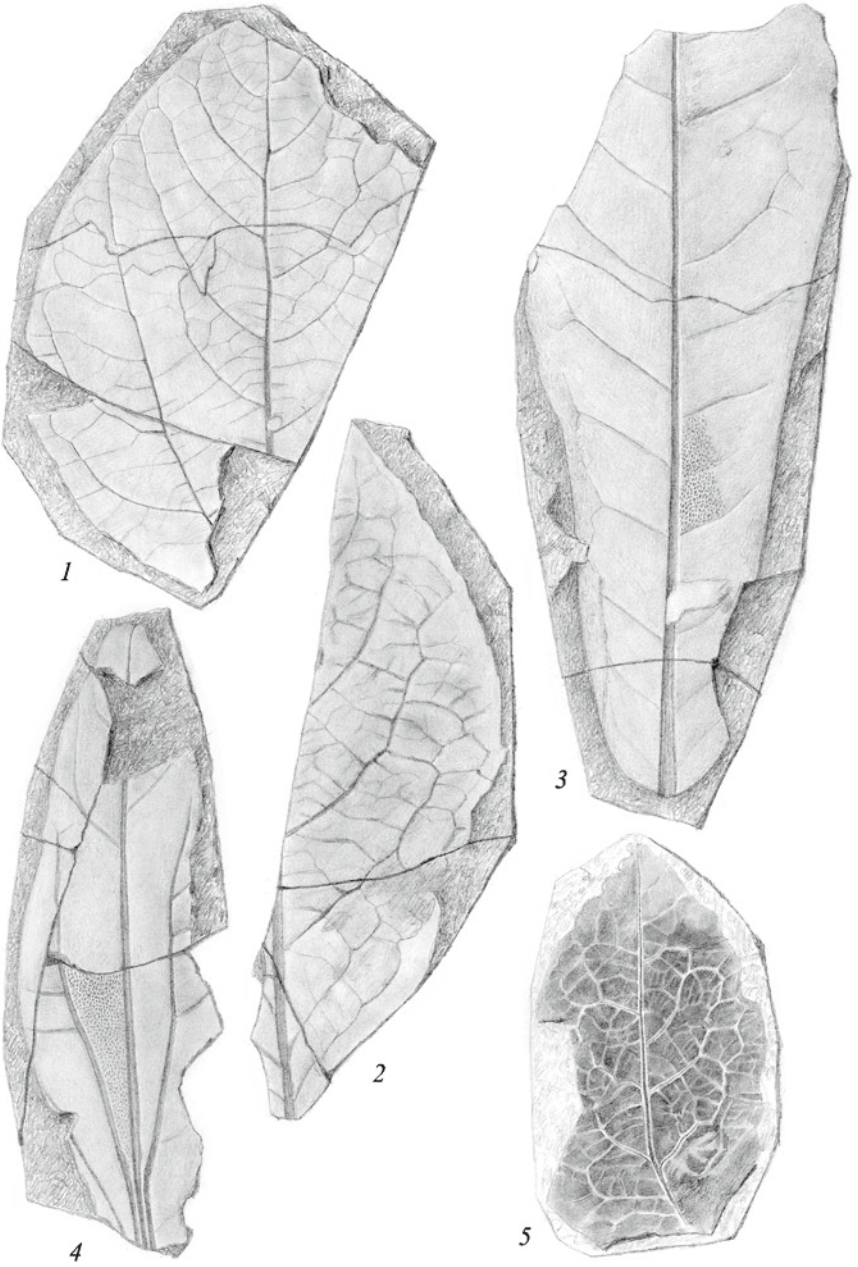



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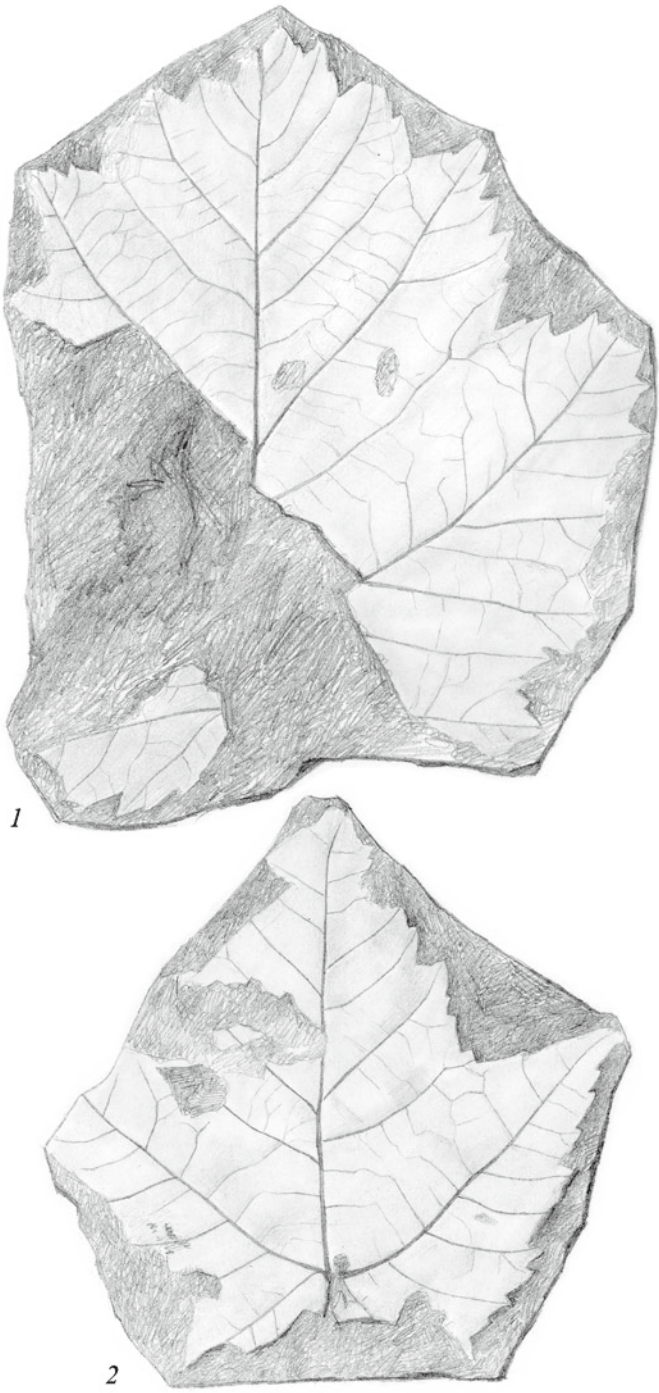



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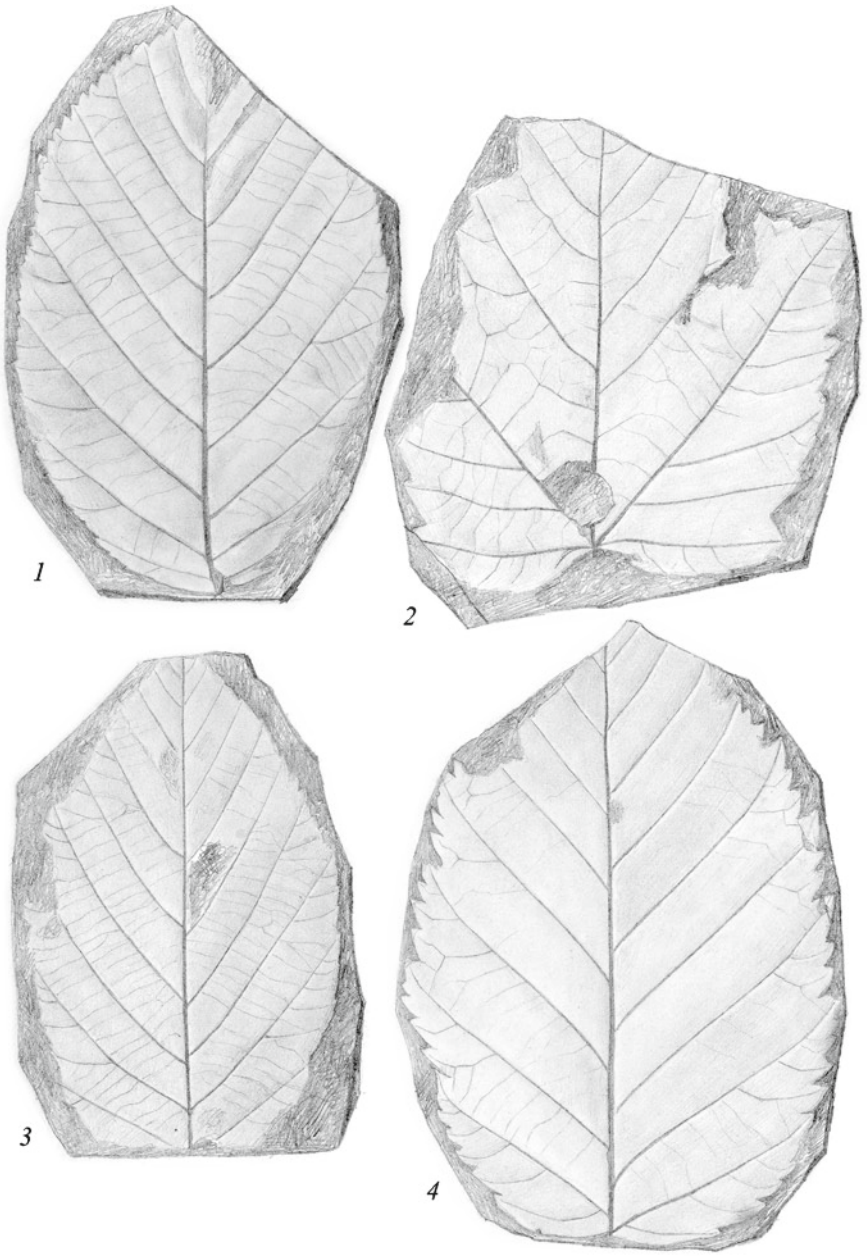



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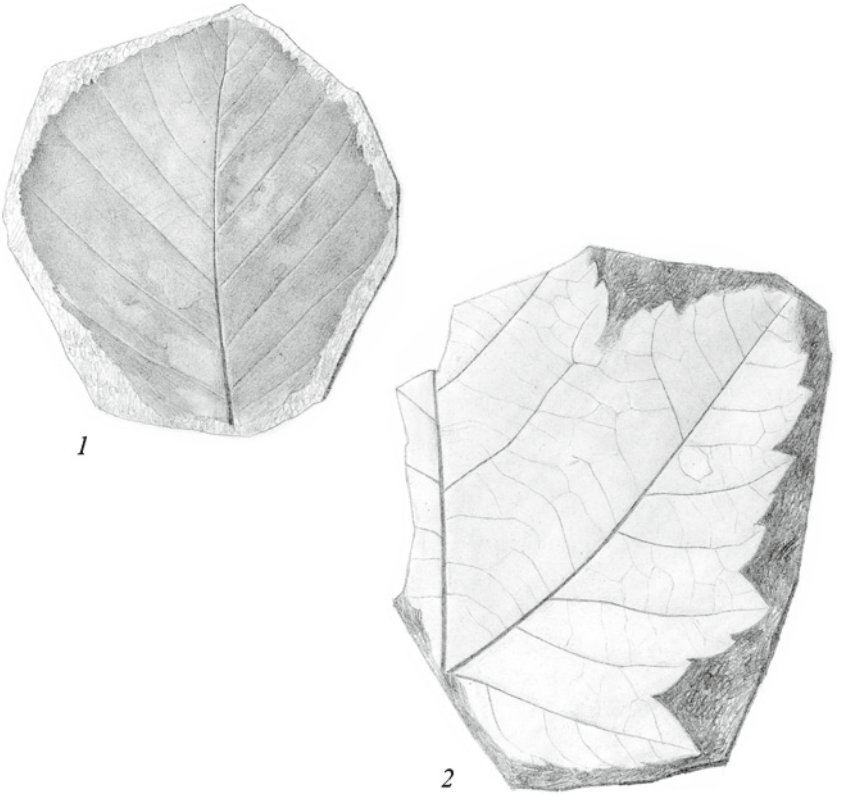



**Plate 14.13** (**a**)




**Plate 14.13 (b)**




**Plate 14.14** (**a**)

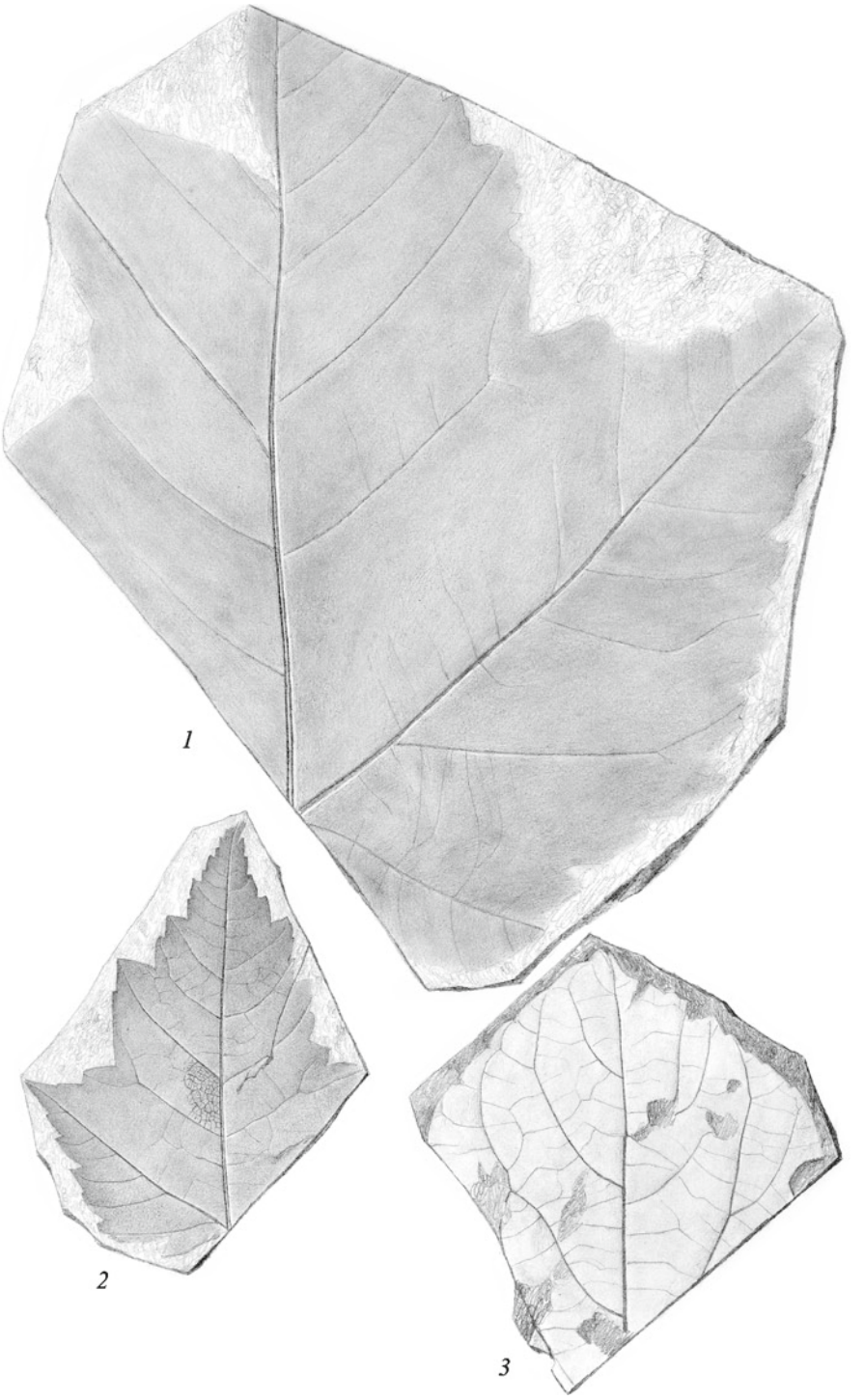



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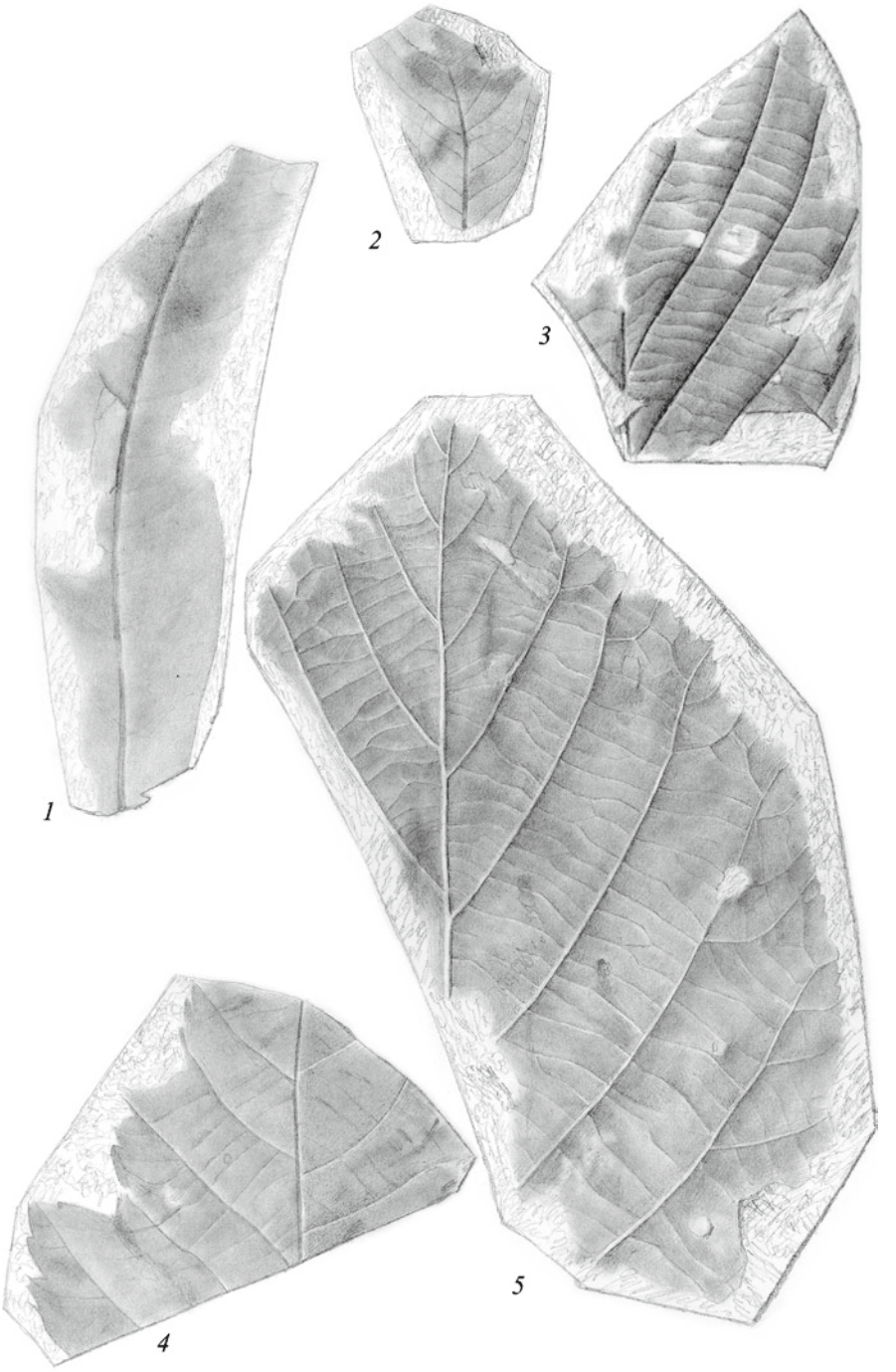



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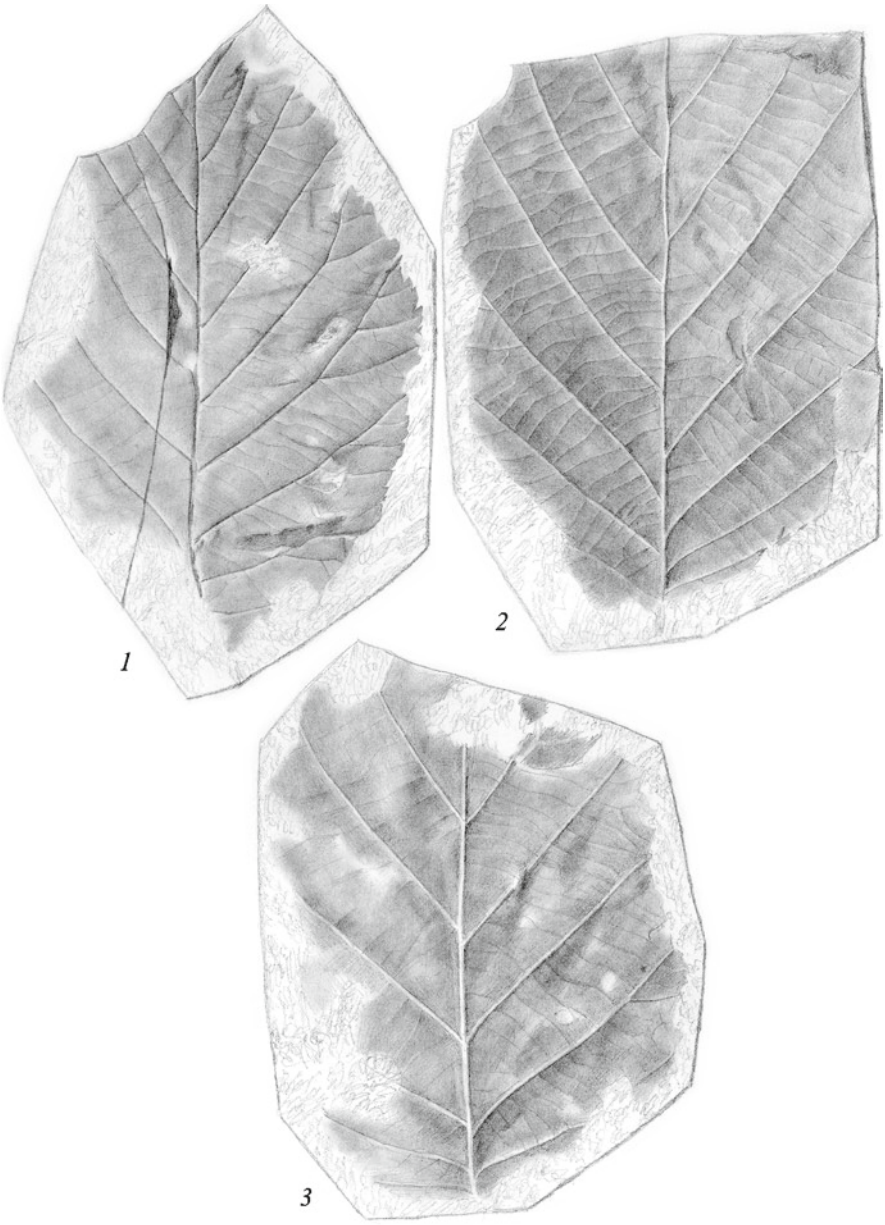



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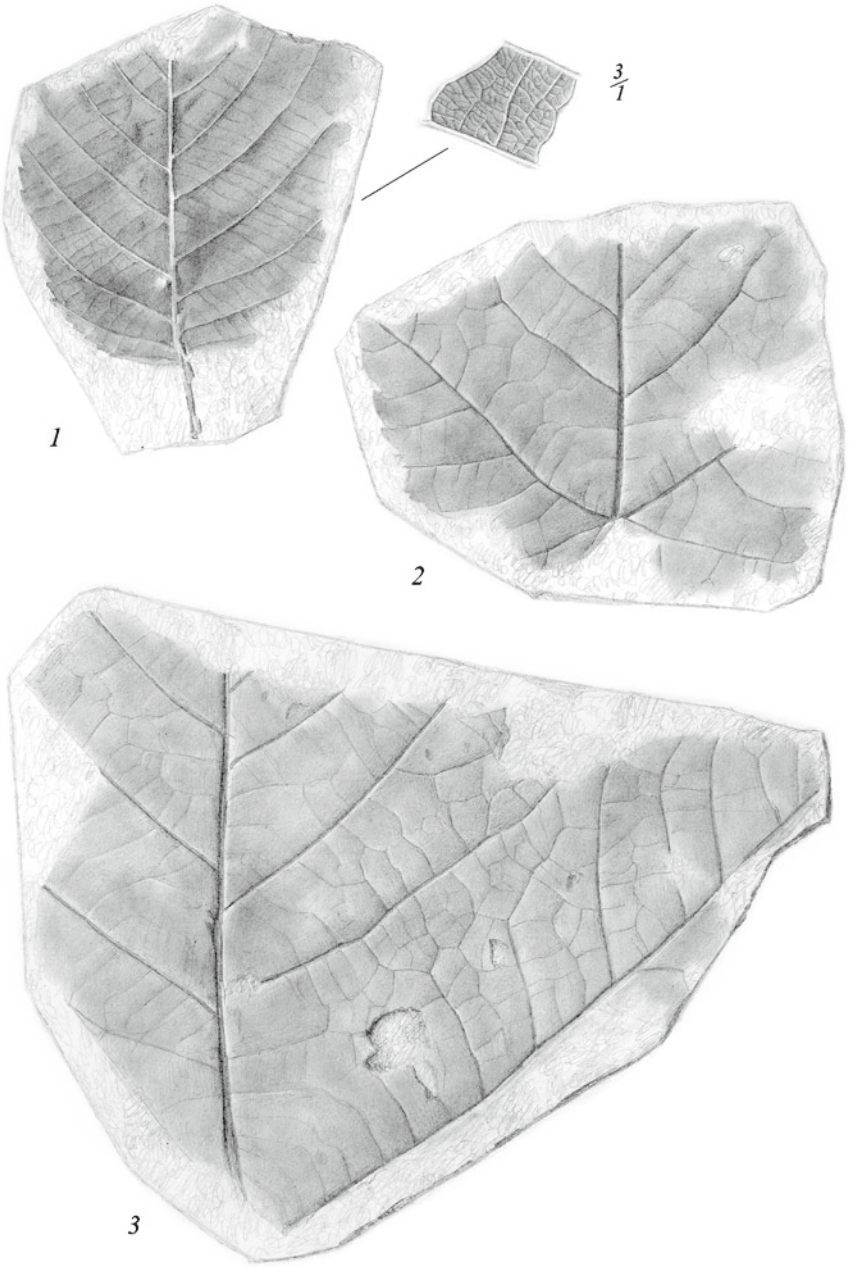



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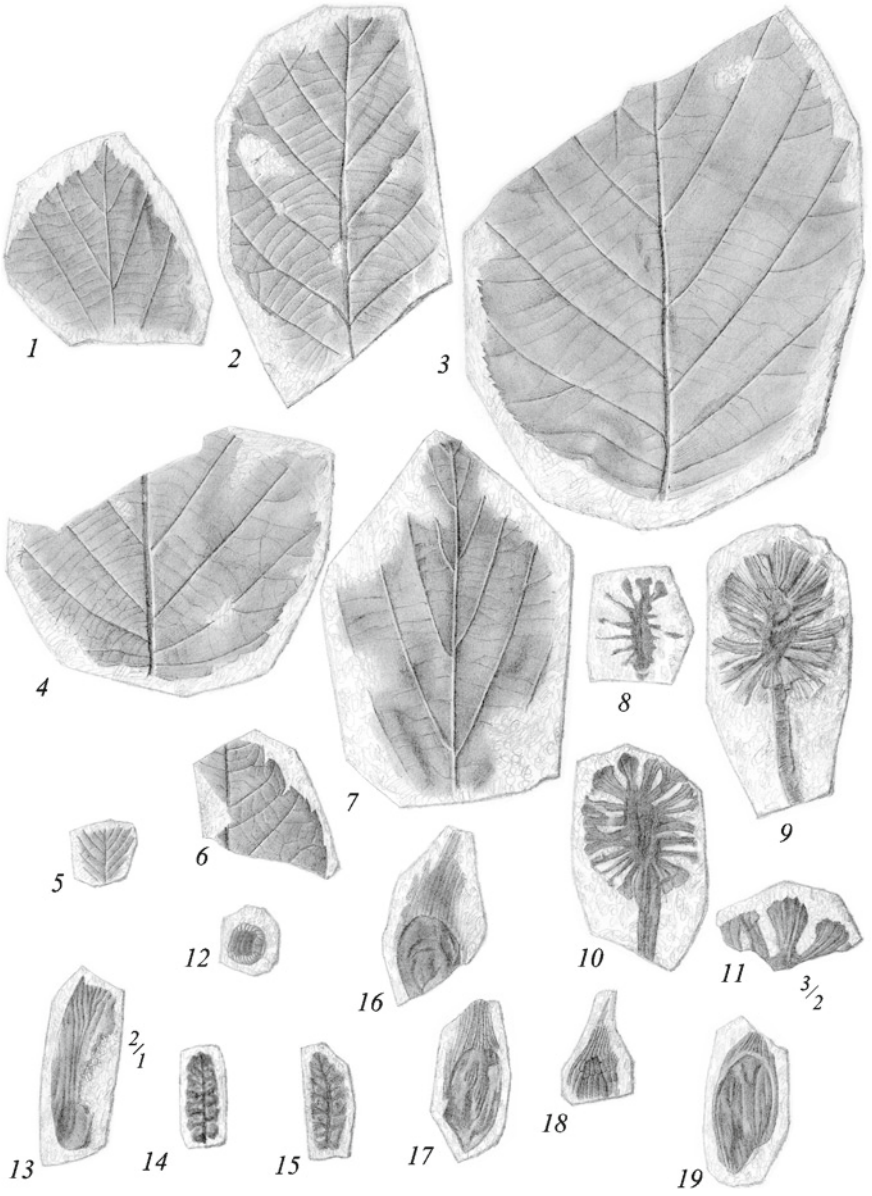



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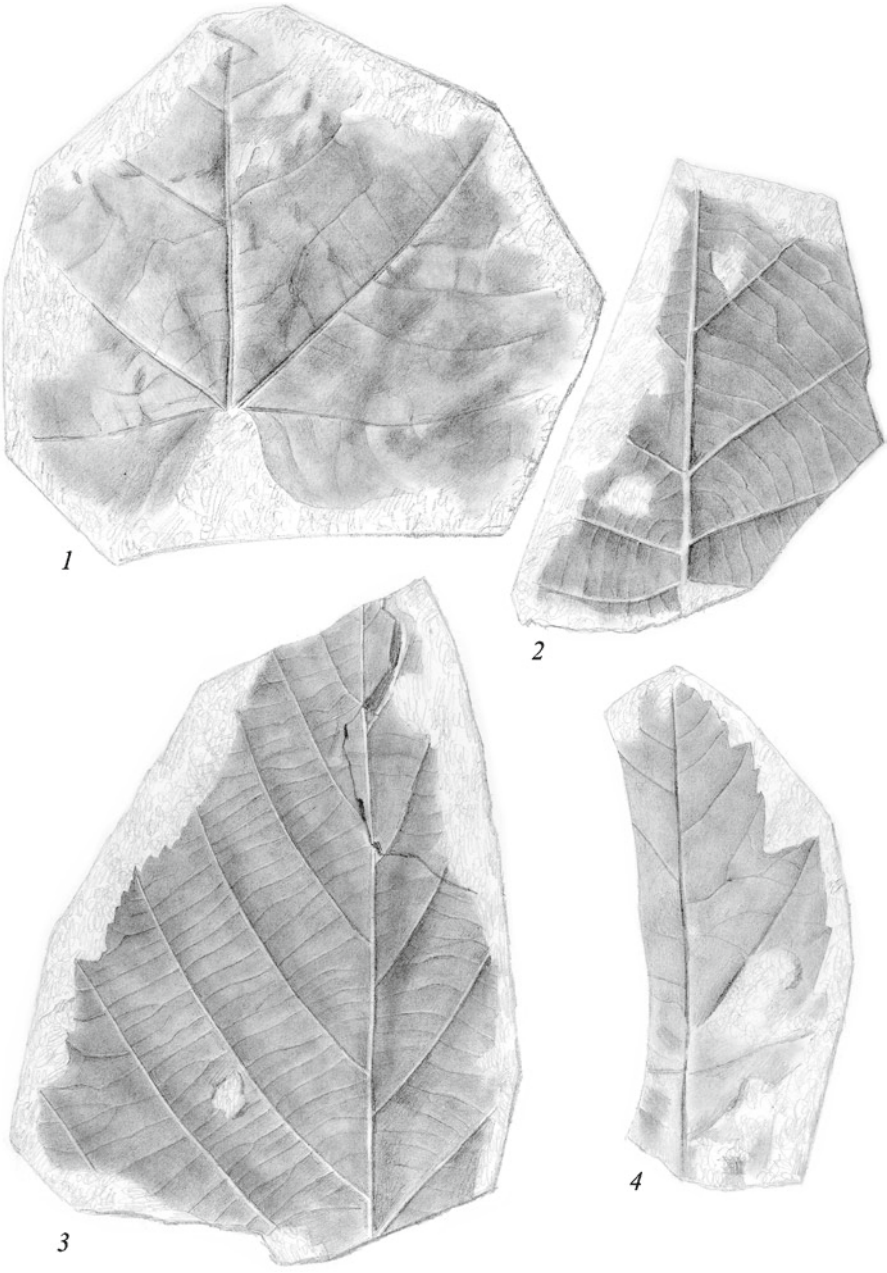



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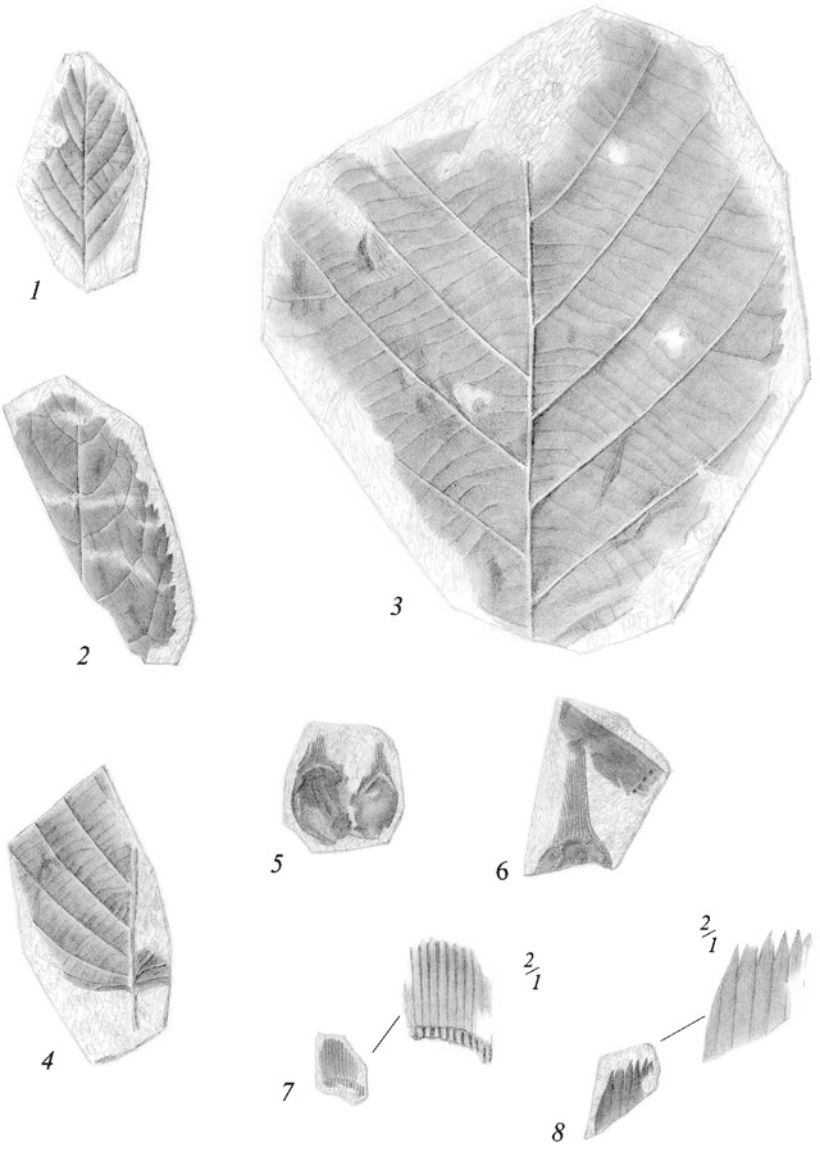



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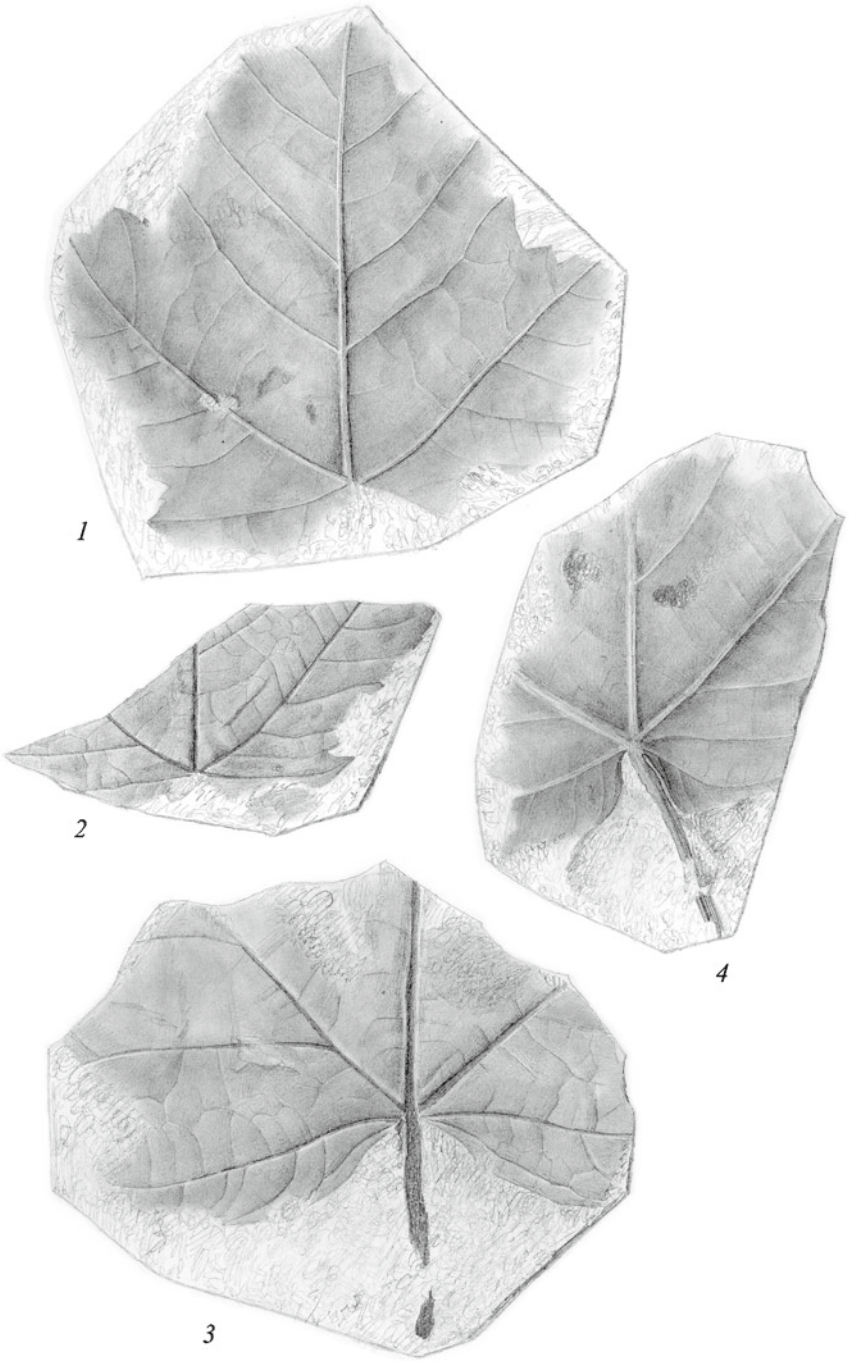



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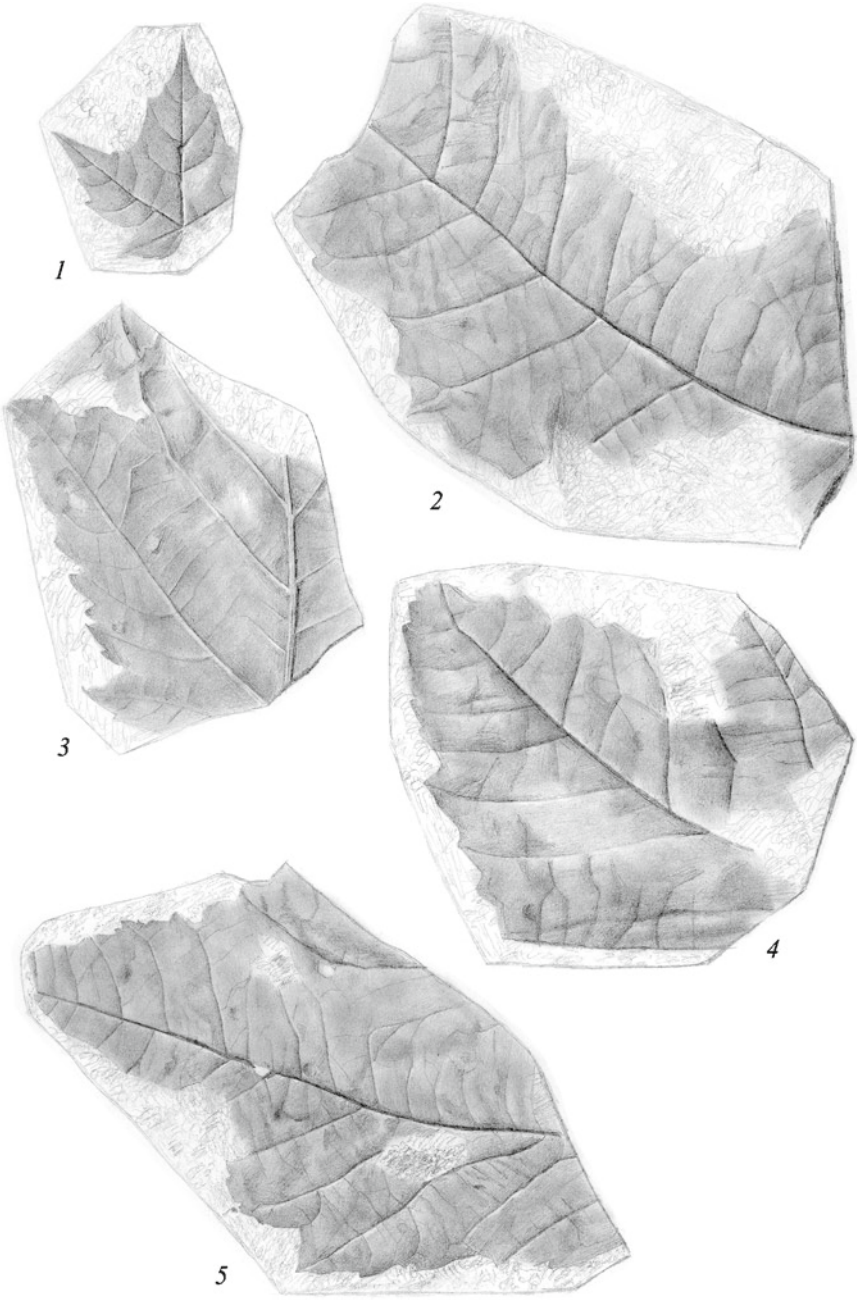



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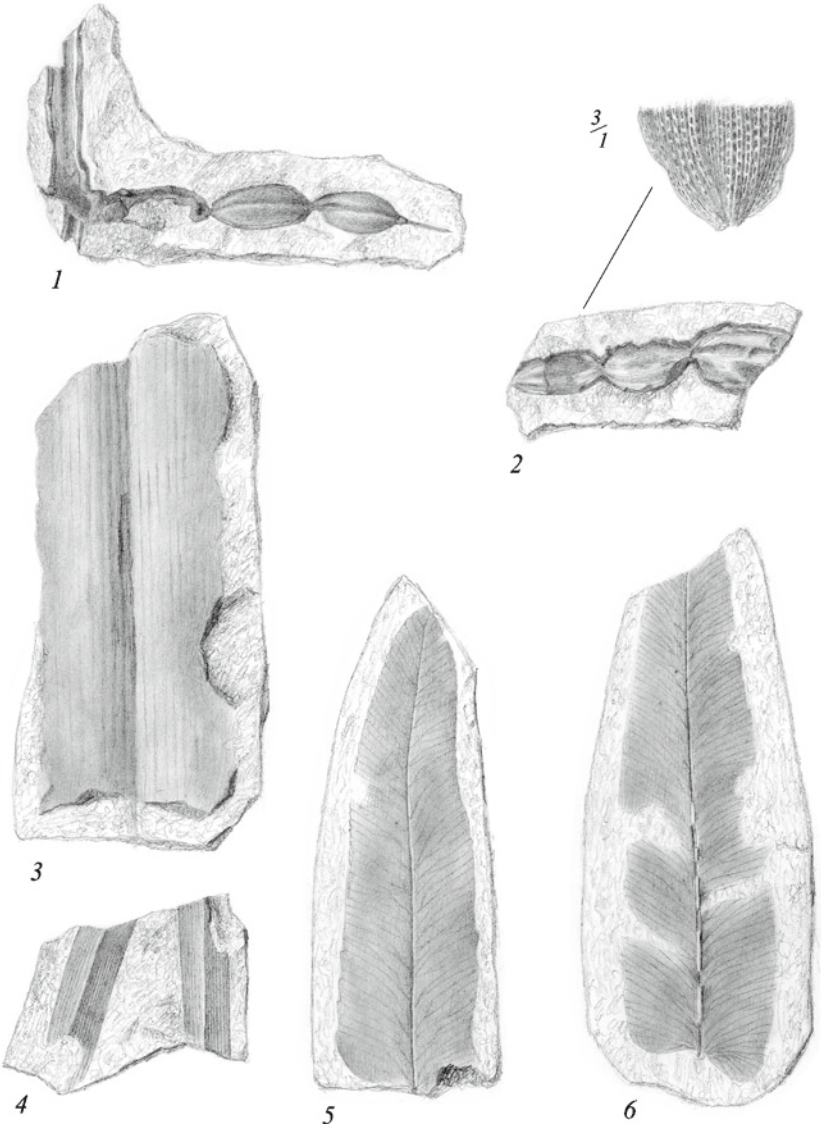



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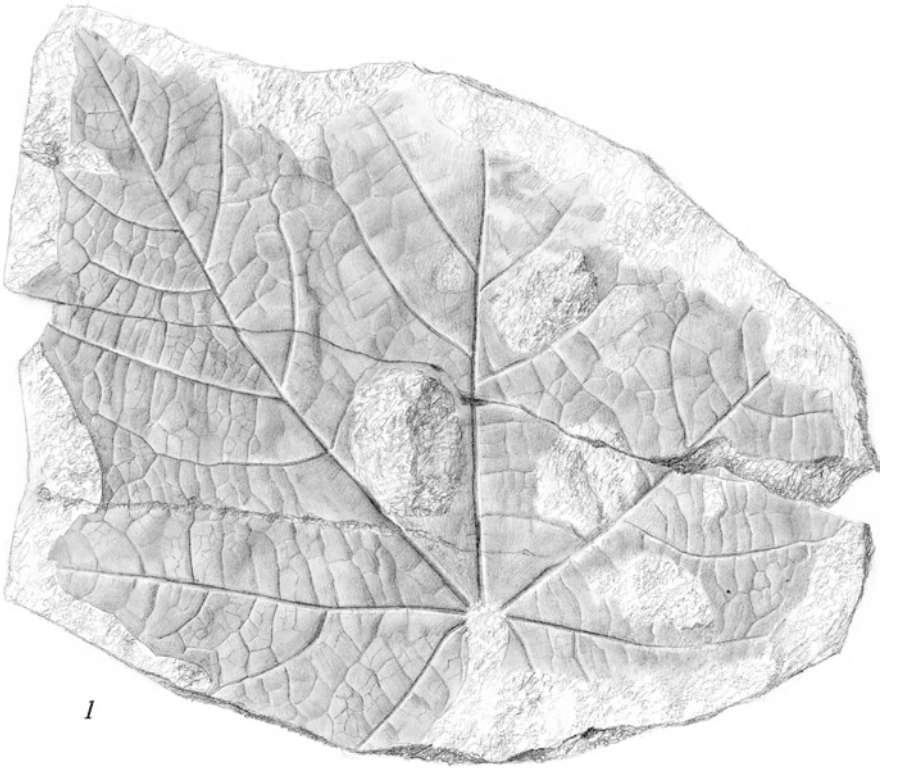



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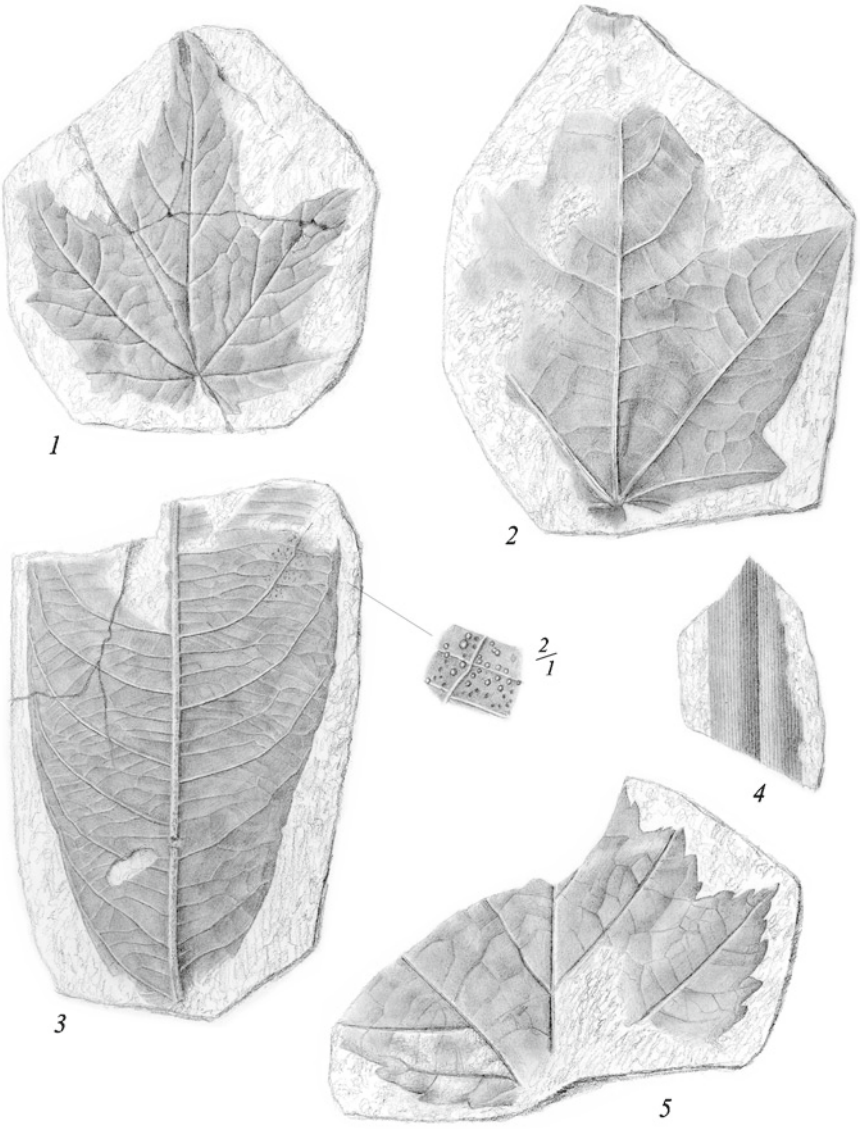



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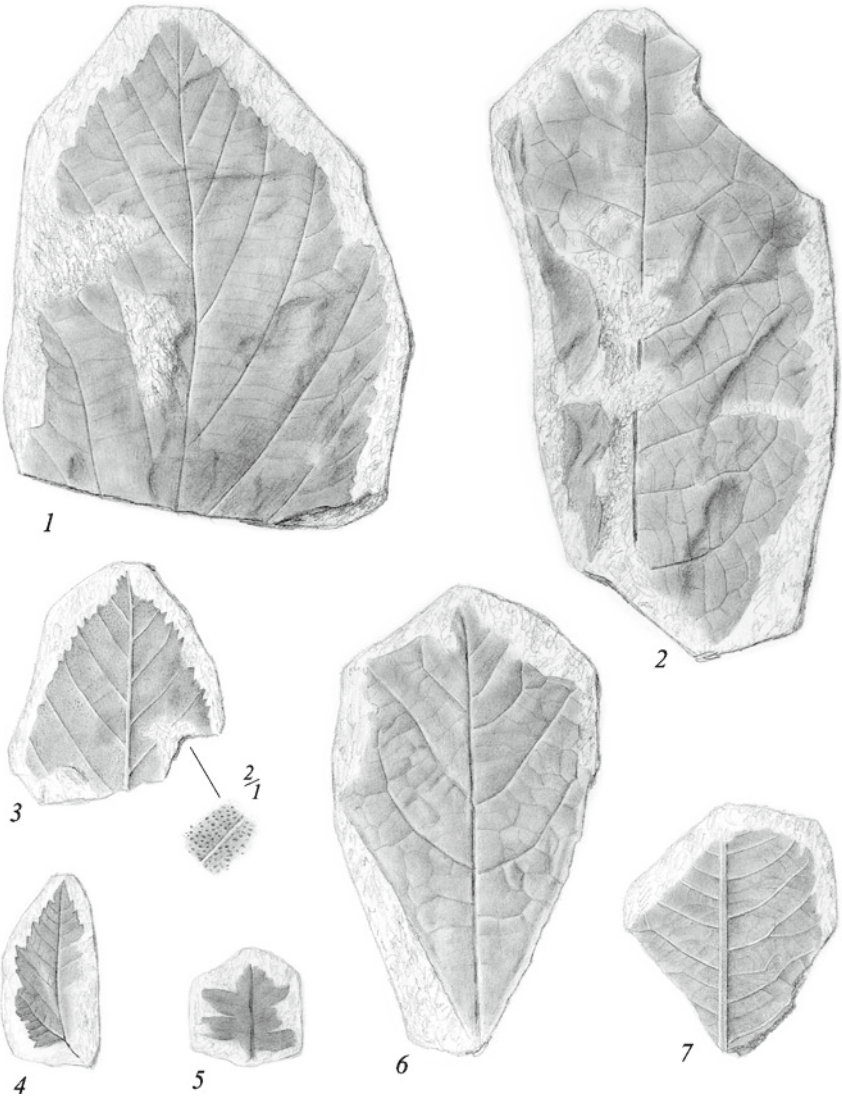



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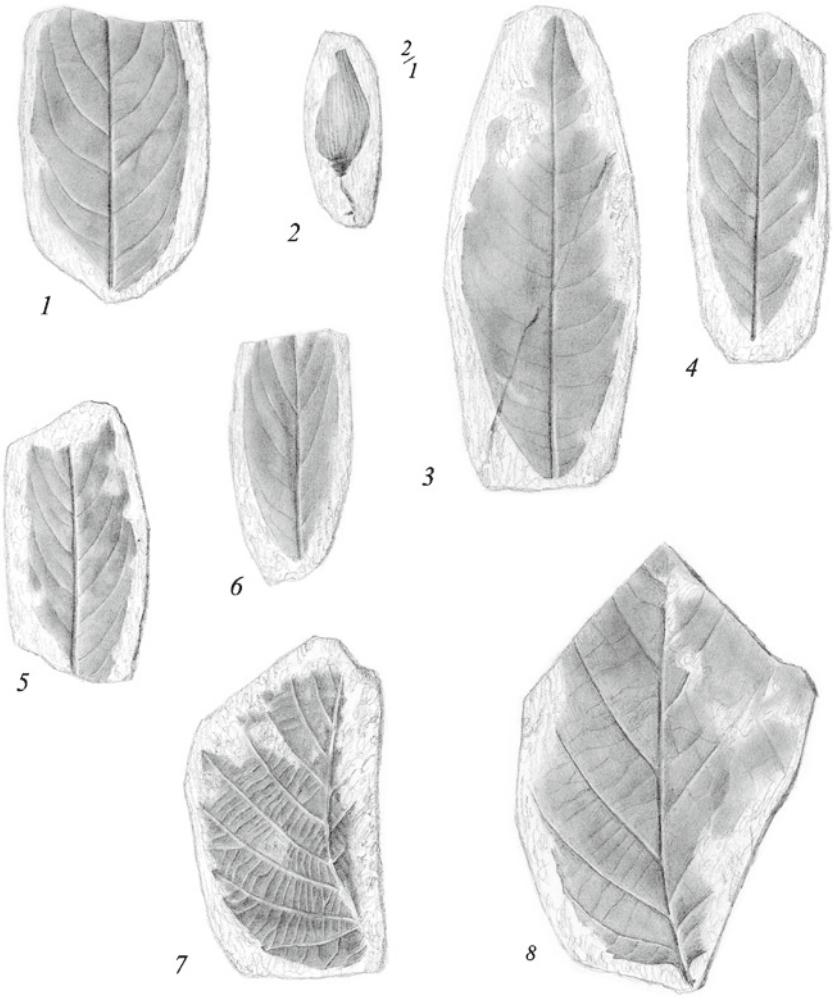



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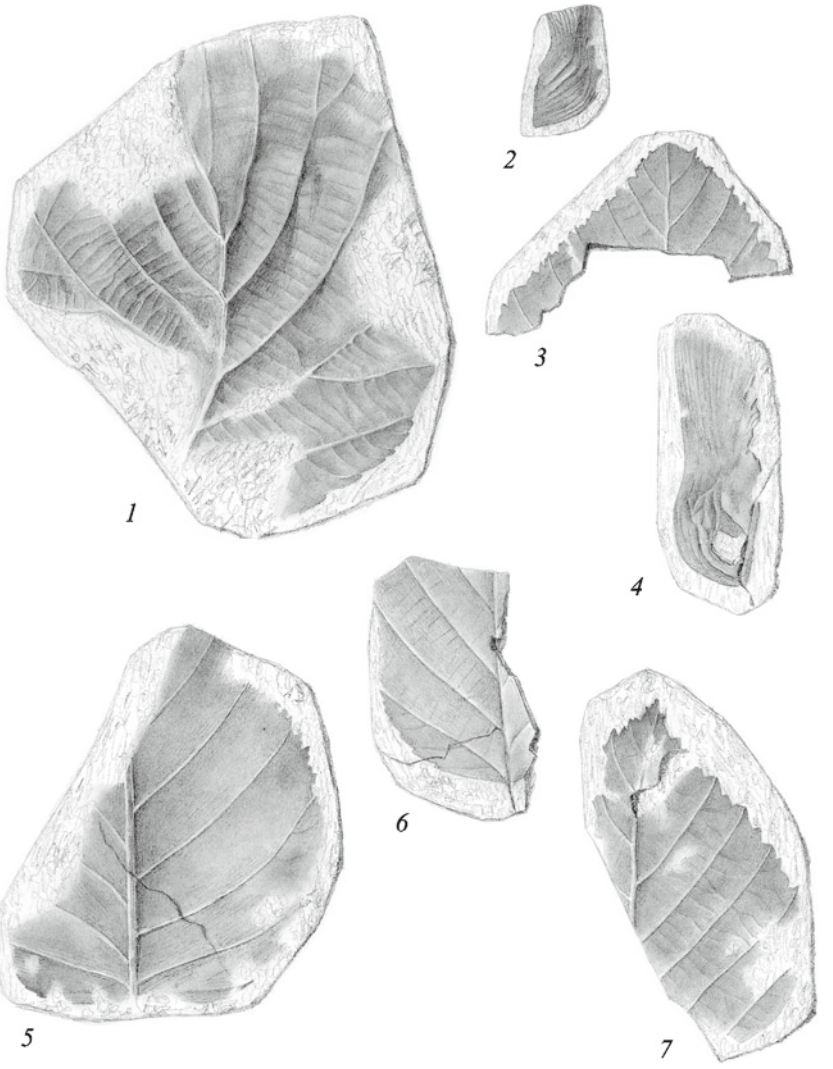



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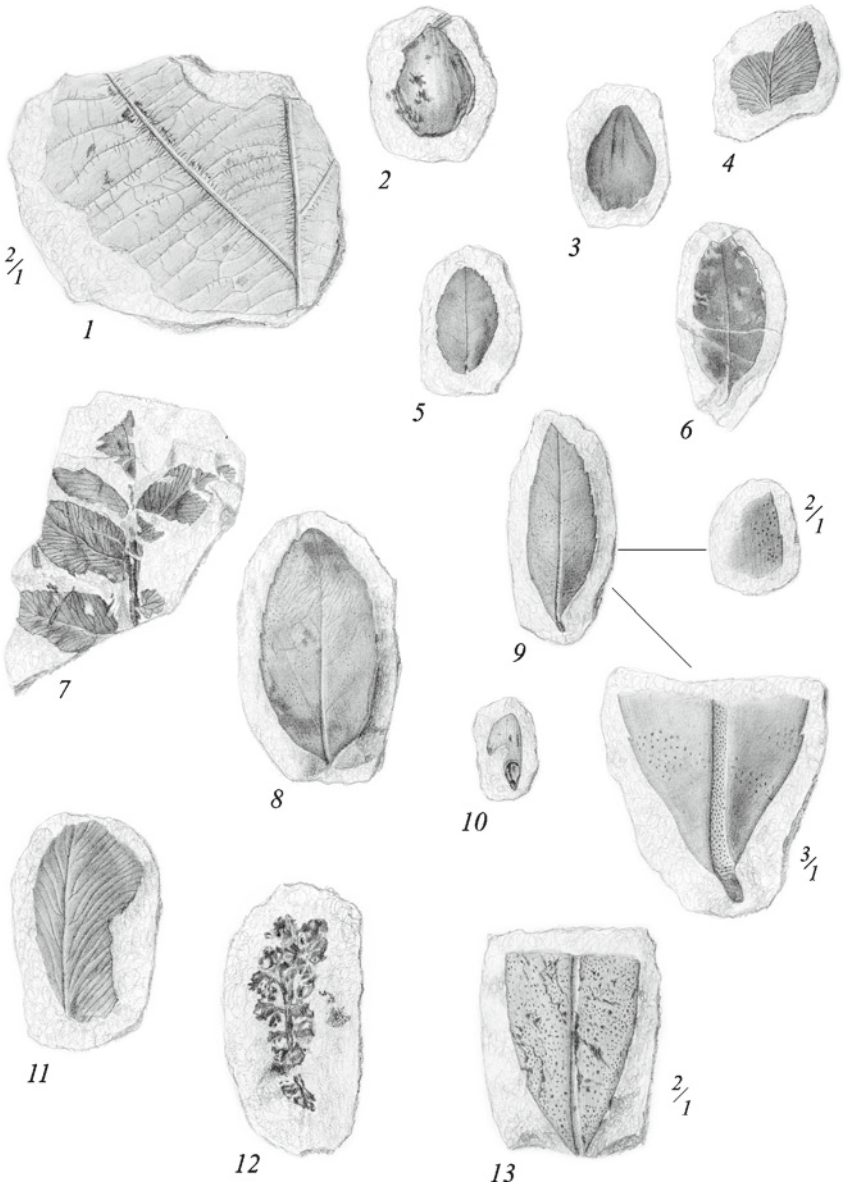



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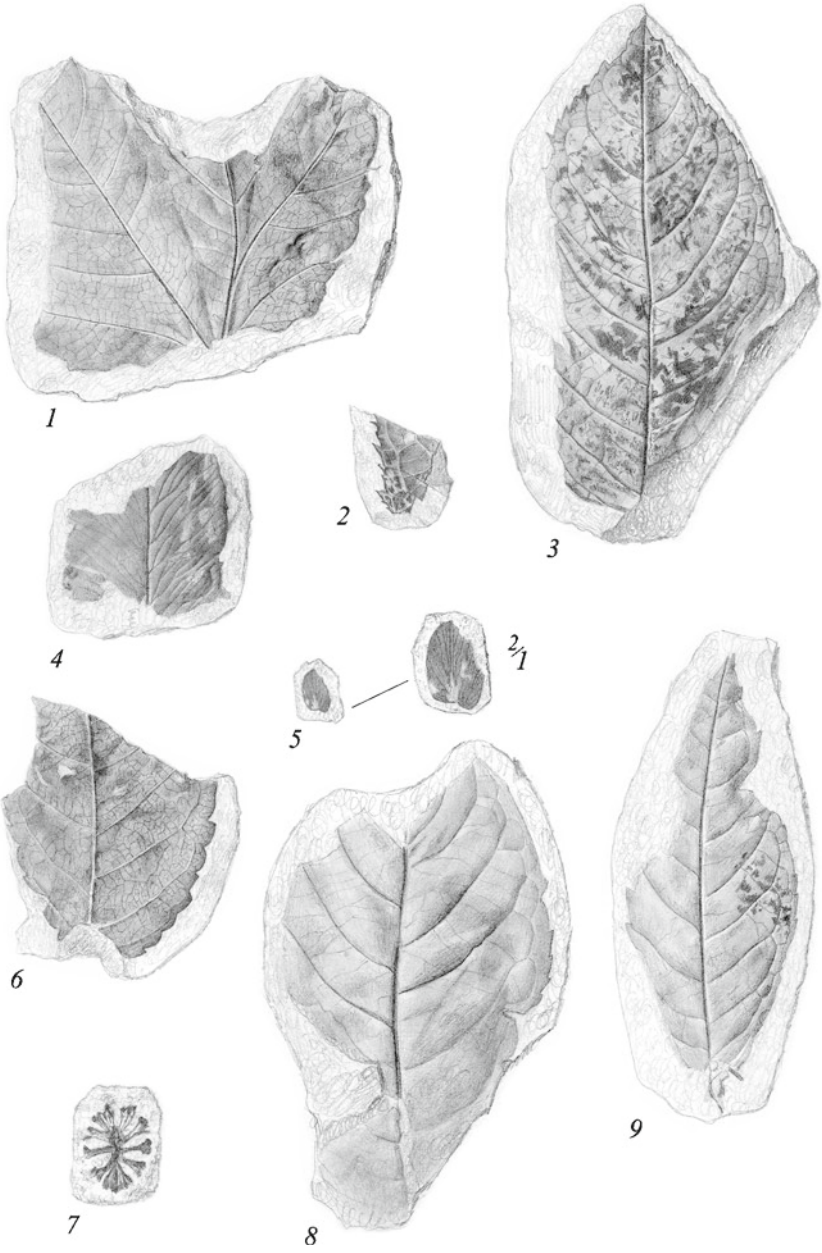



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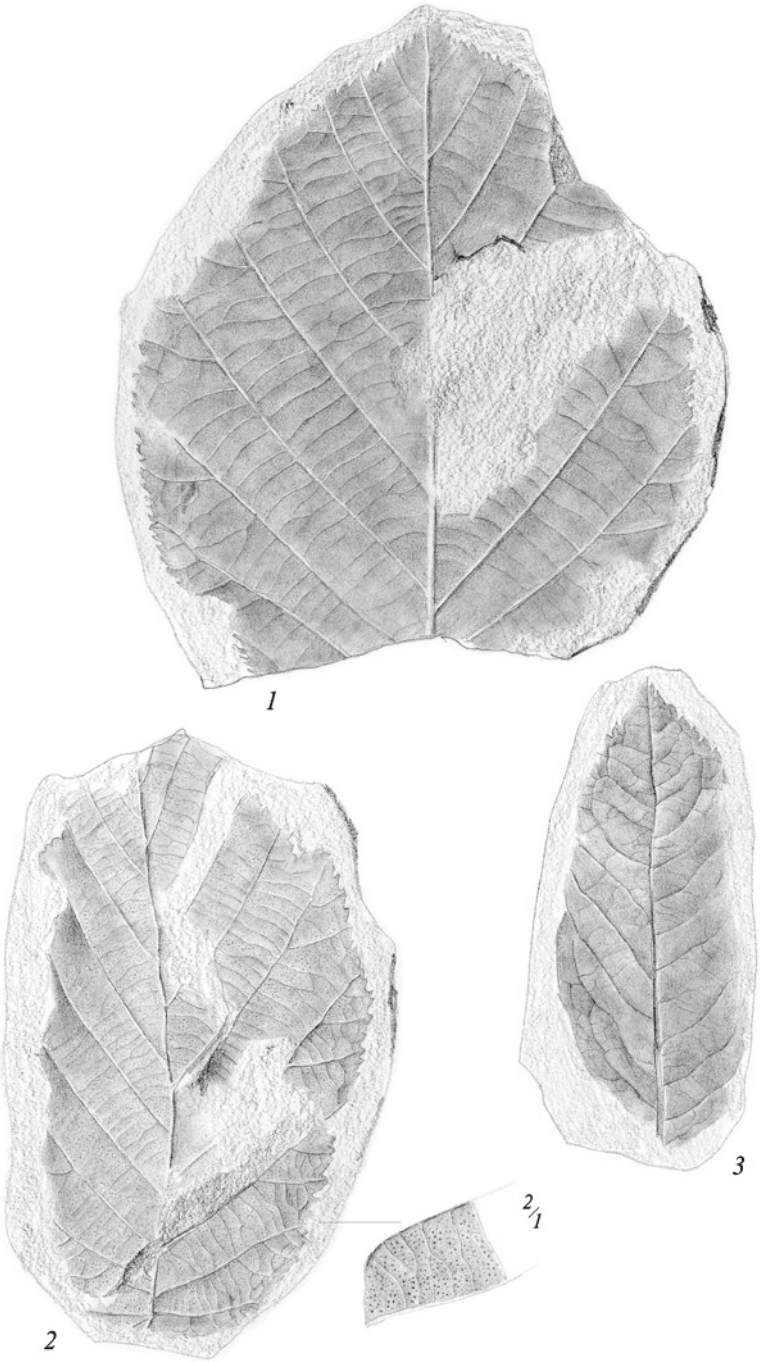



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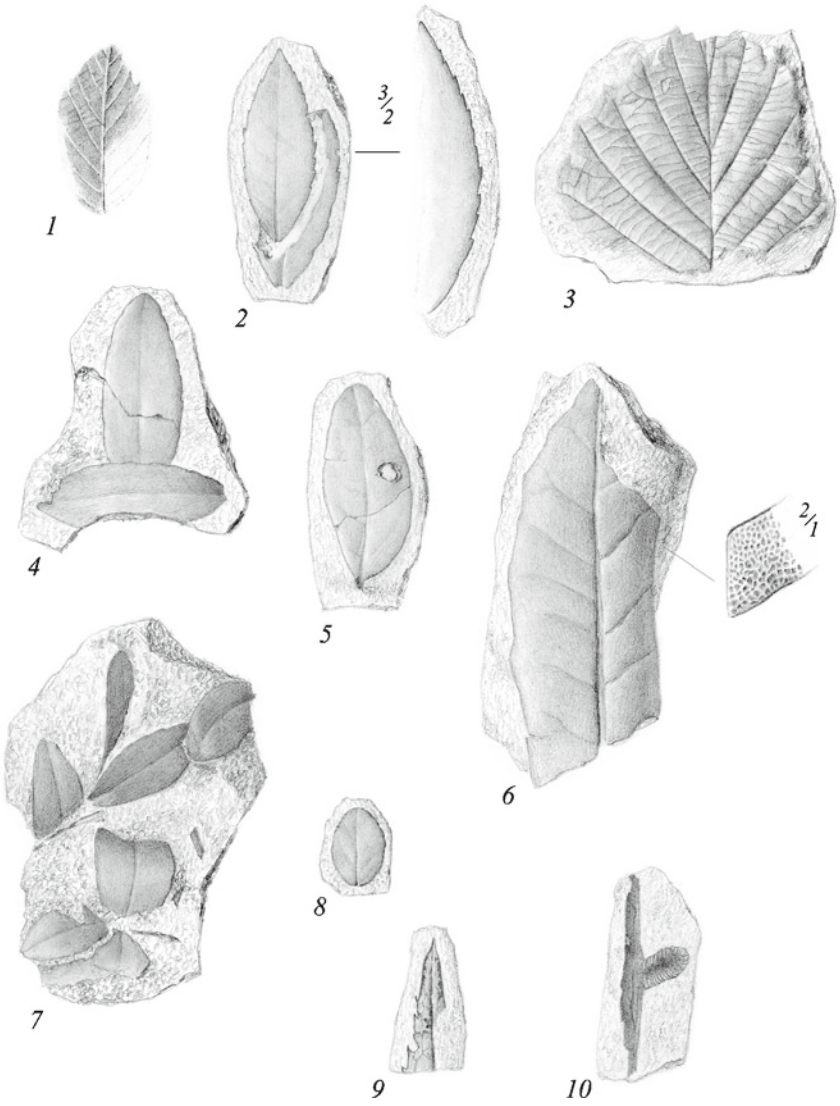



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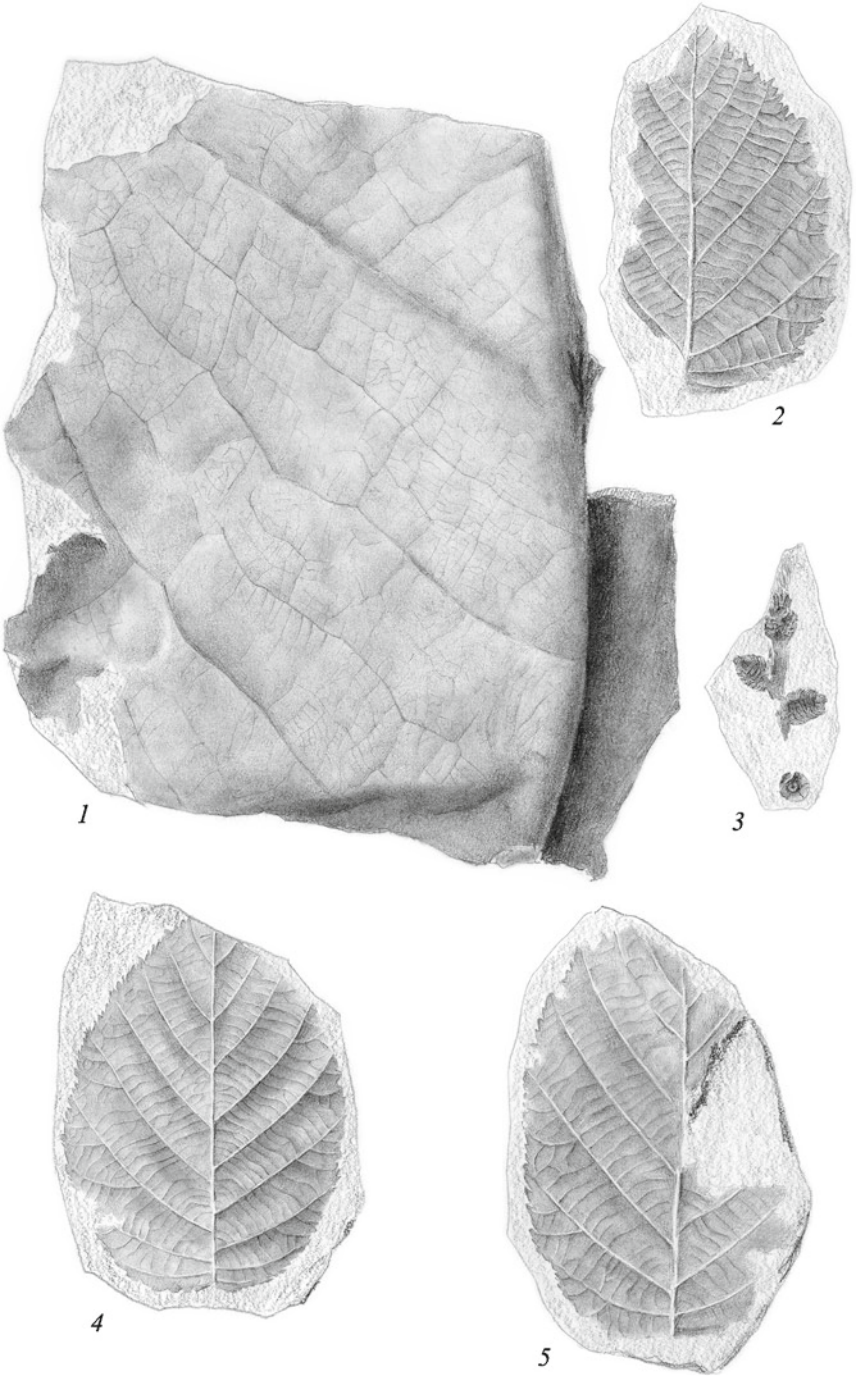



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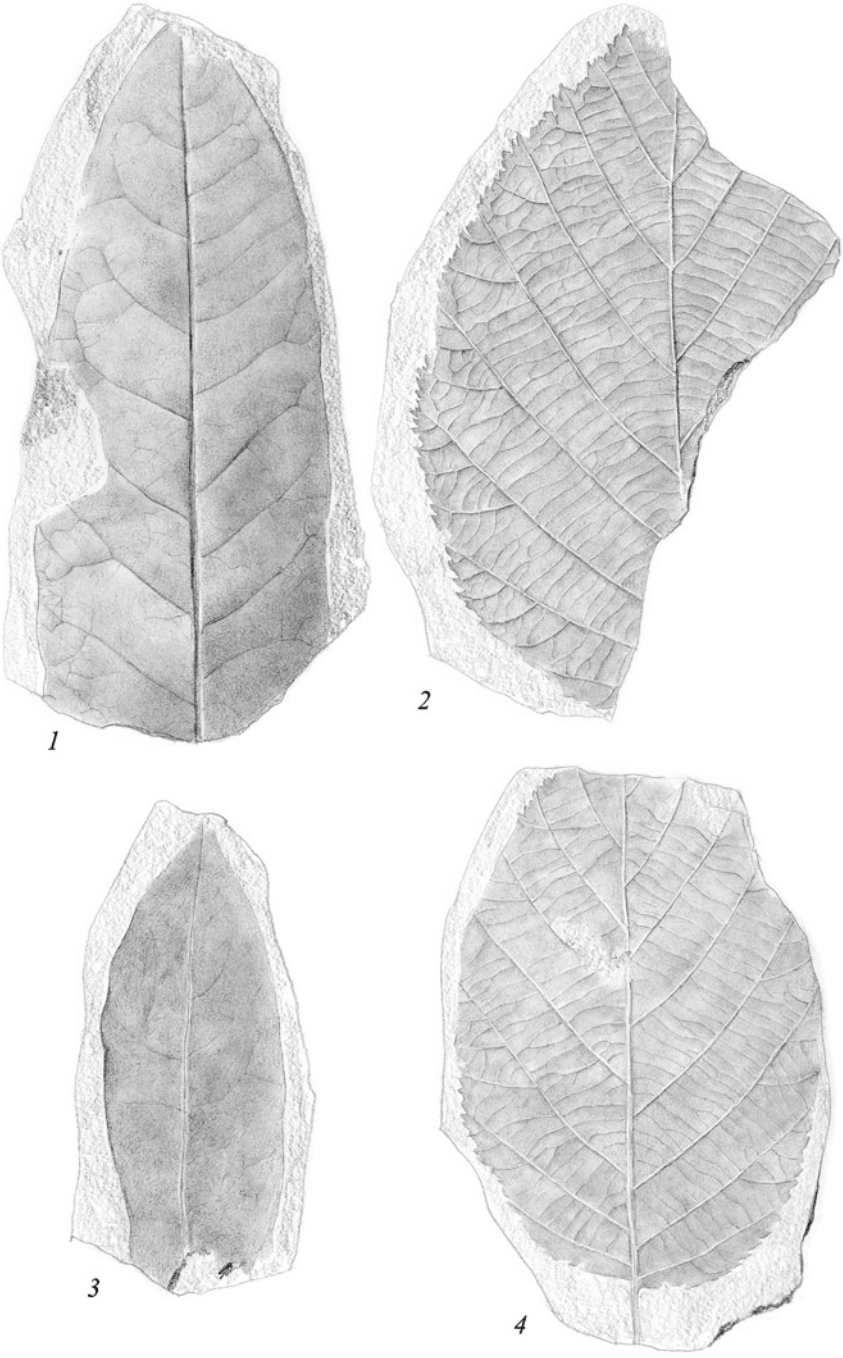



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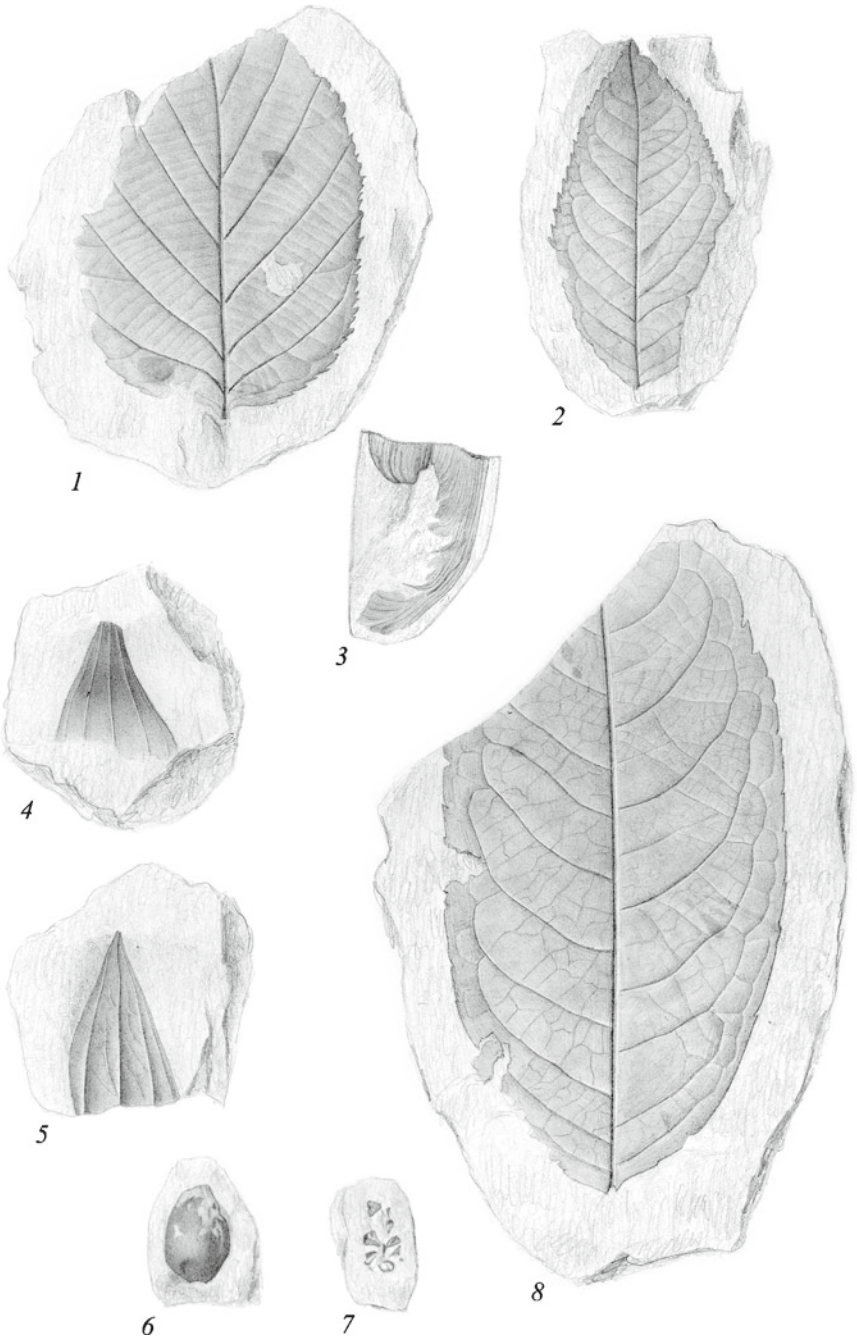



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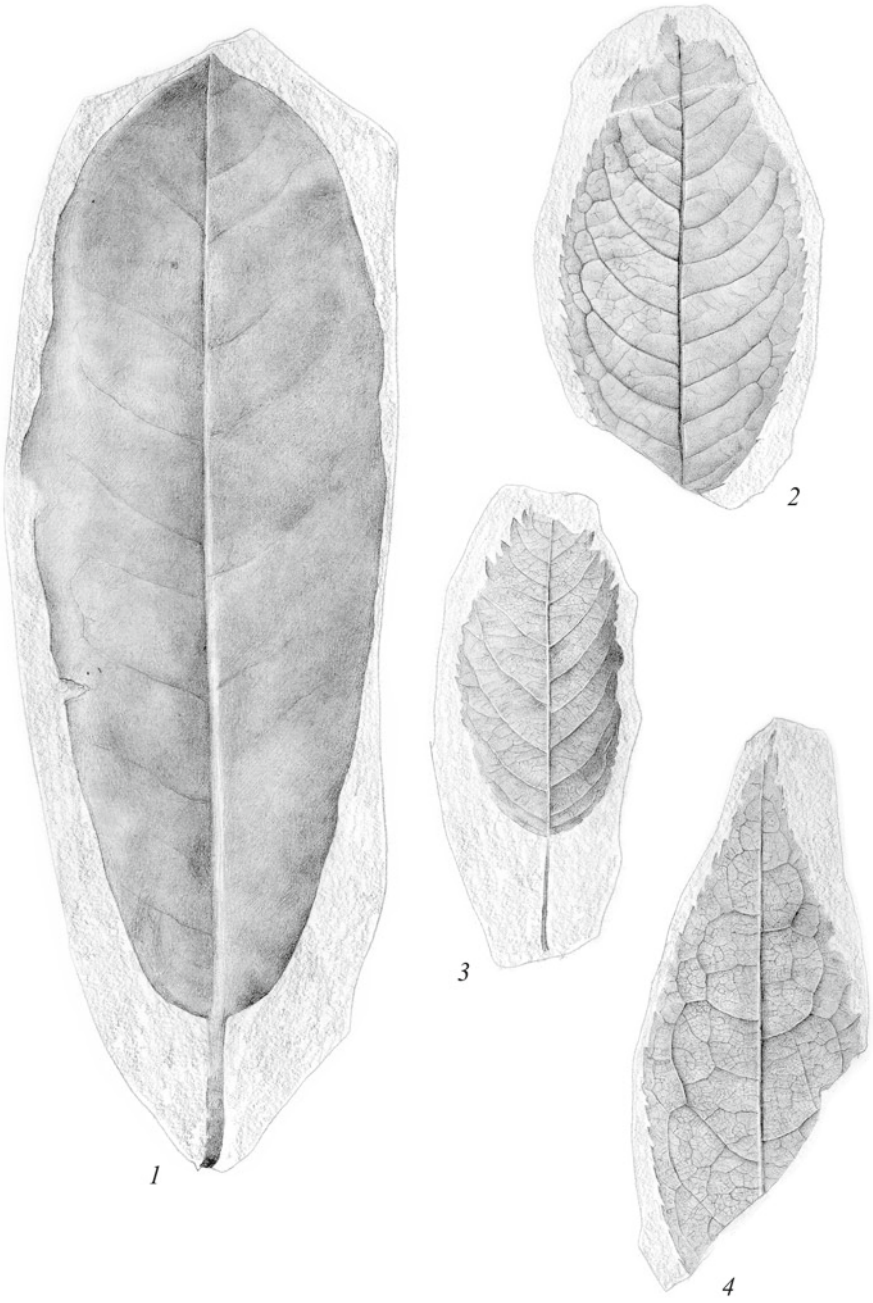



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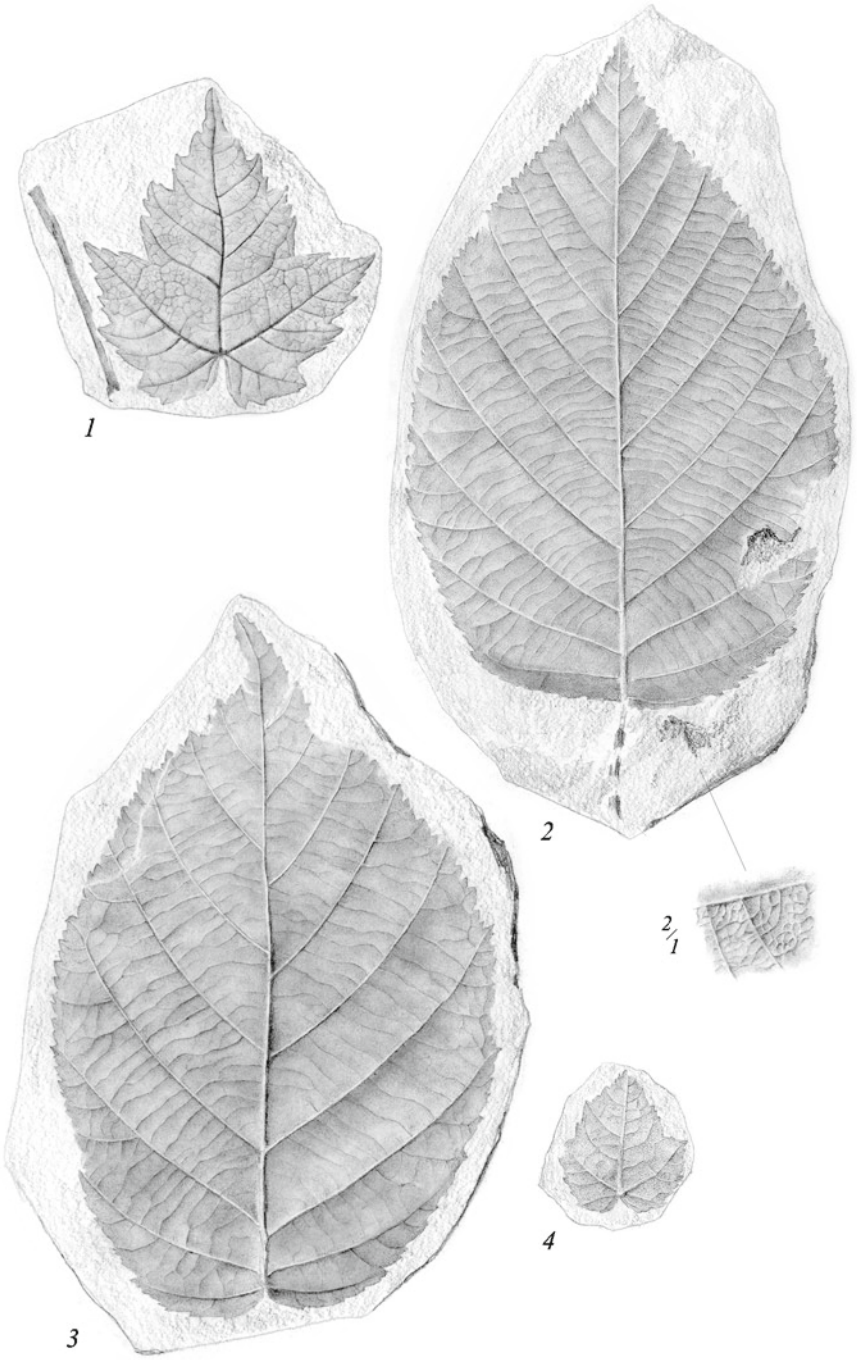



**Plate 14.26 (b)**

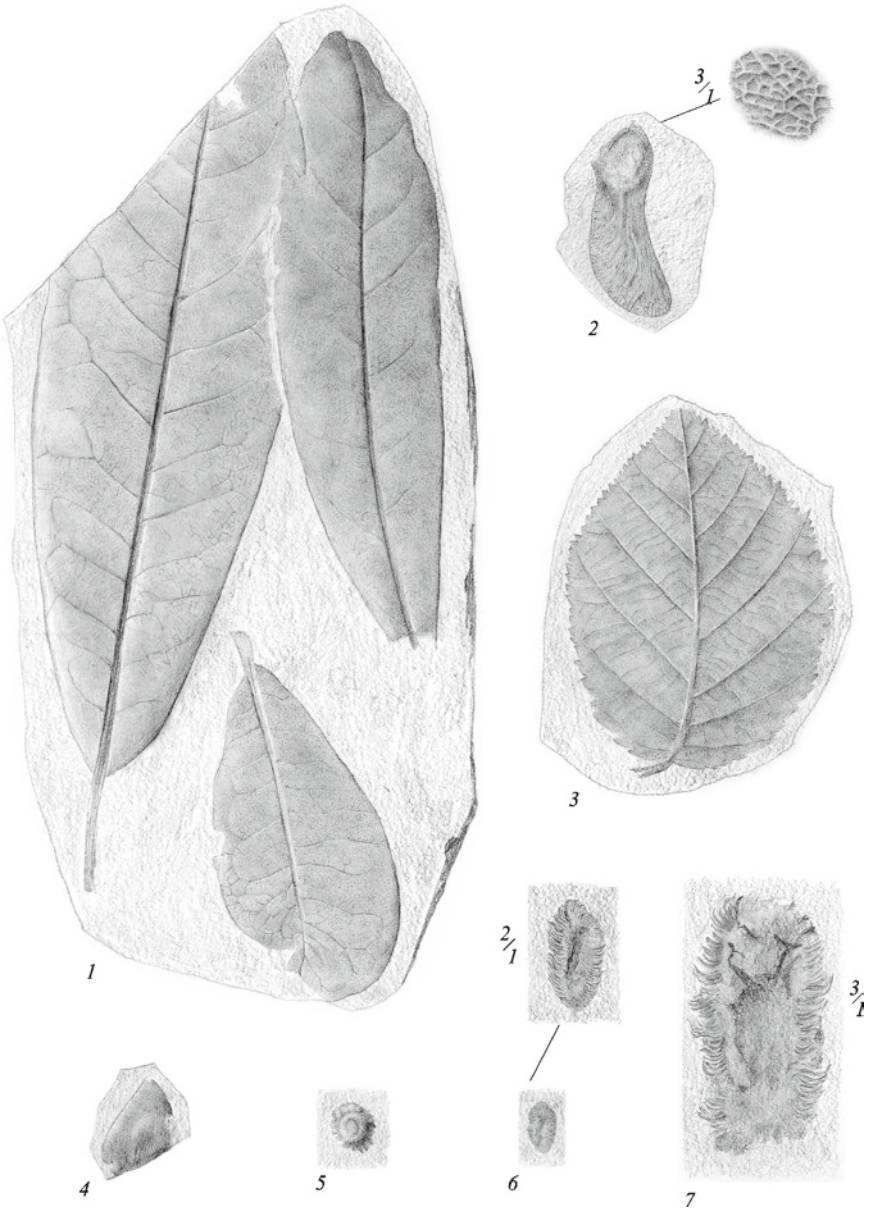



**Plate 14.27** (**a**)

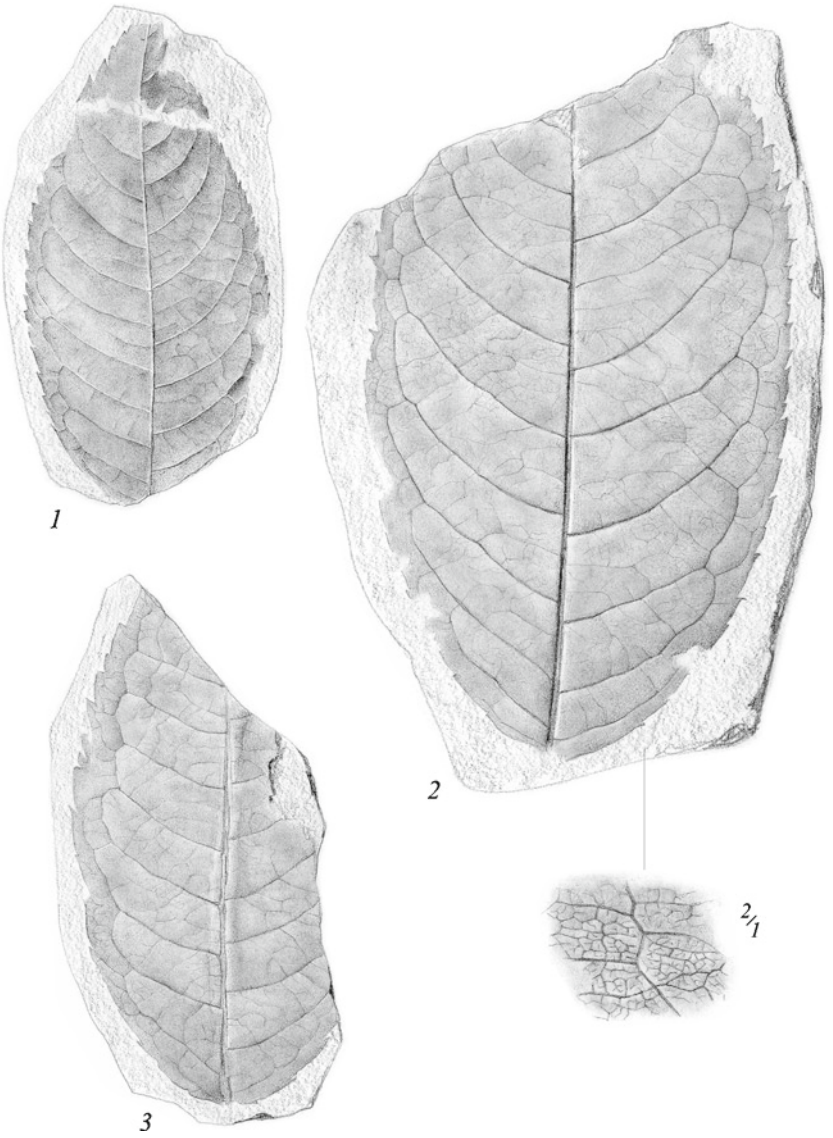



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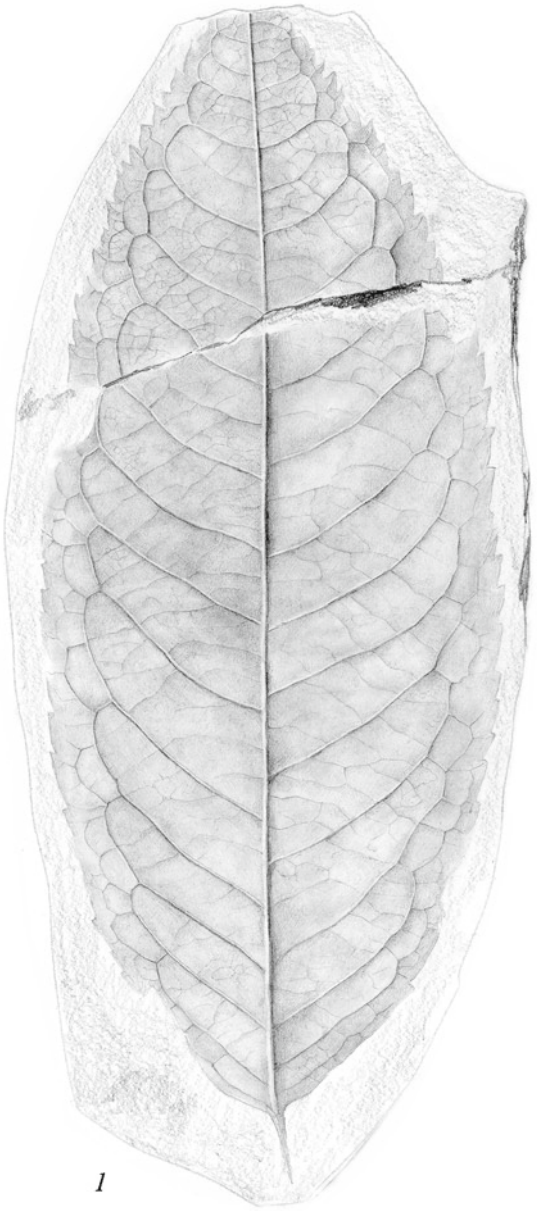



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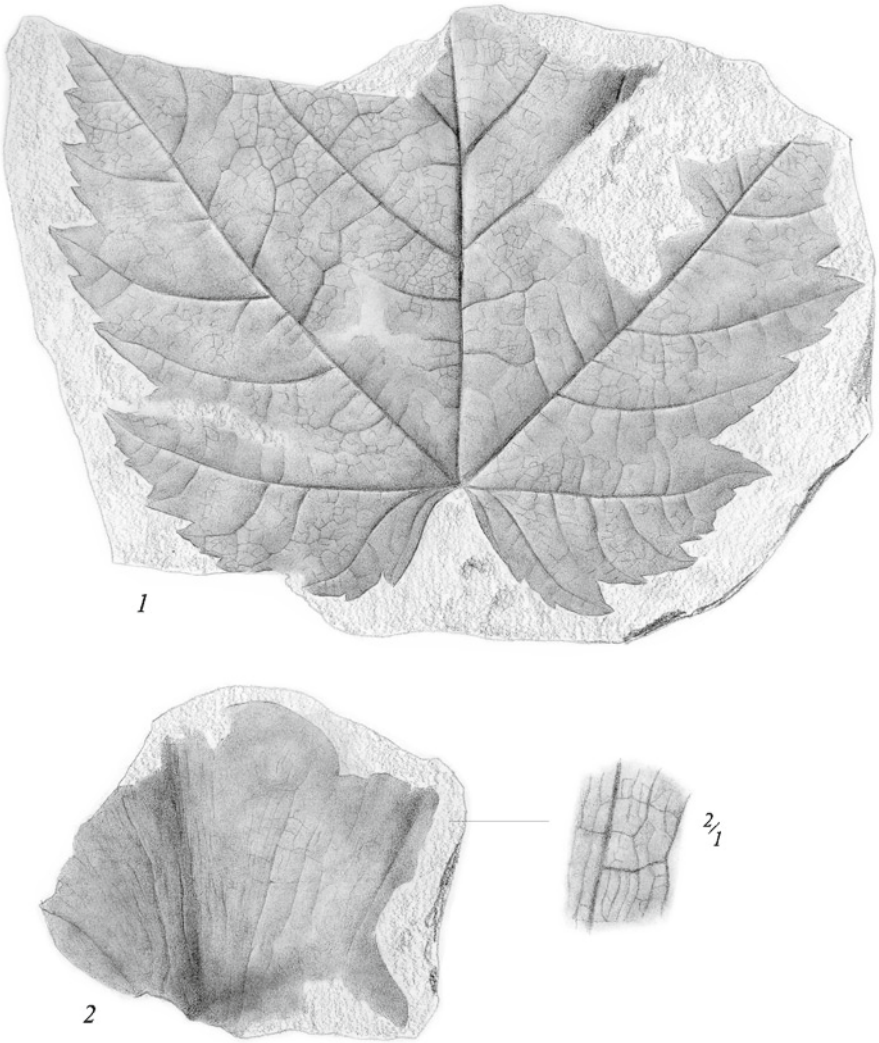



**Plate 14.29 (a)**

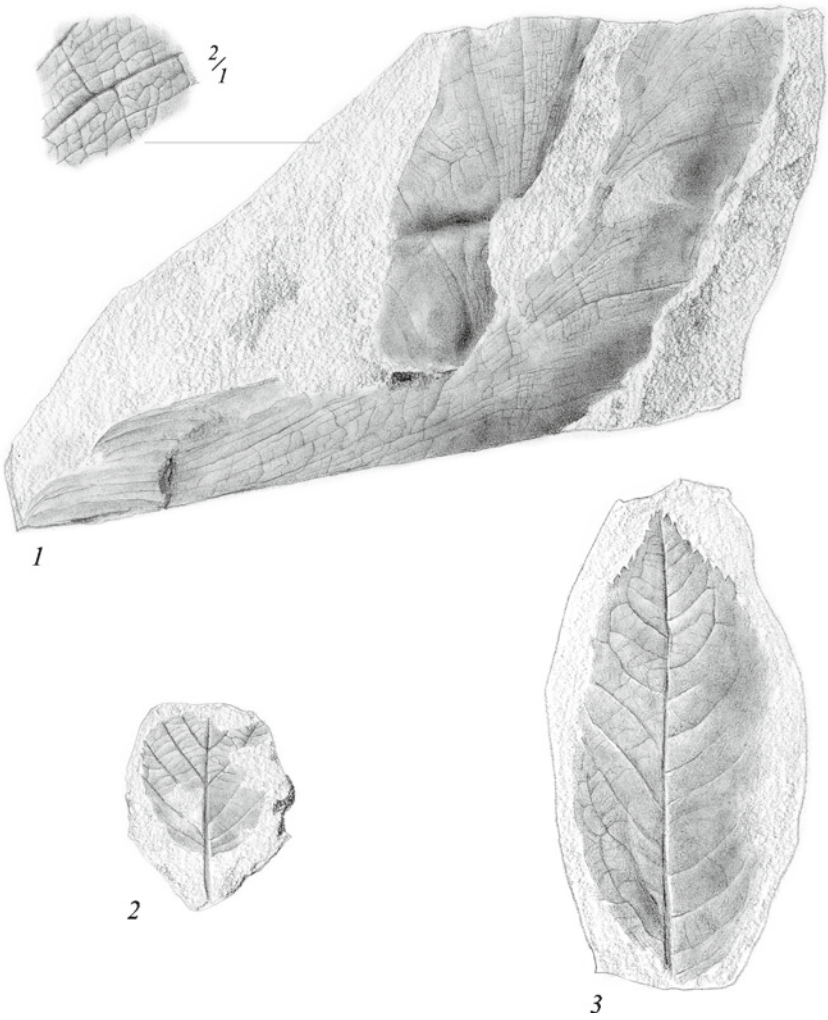



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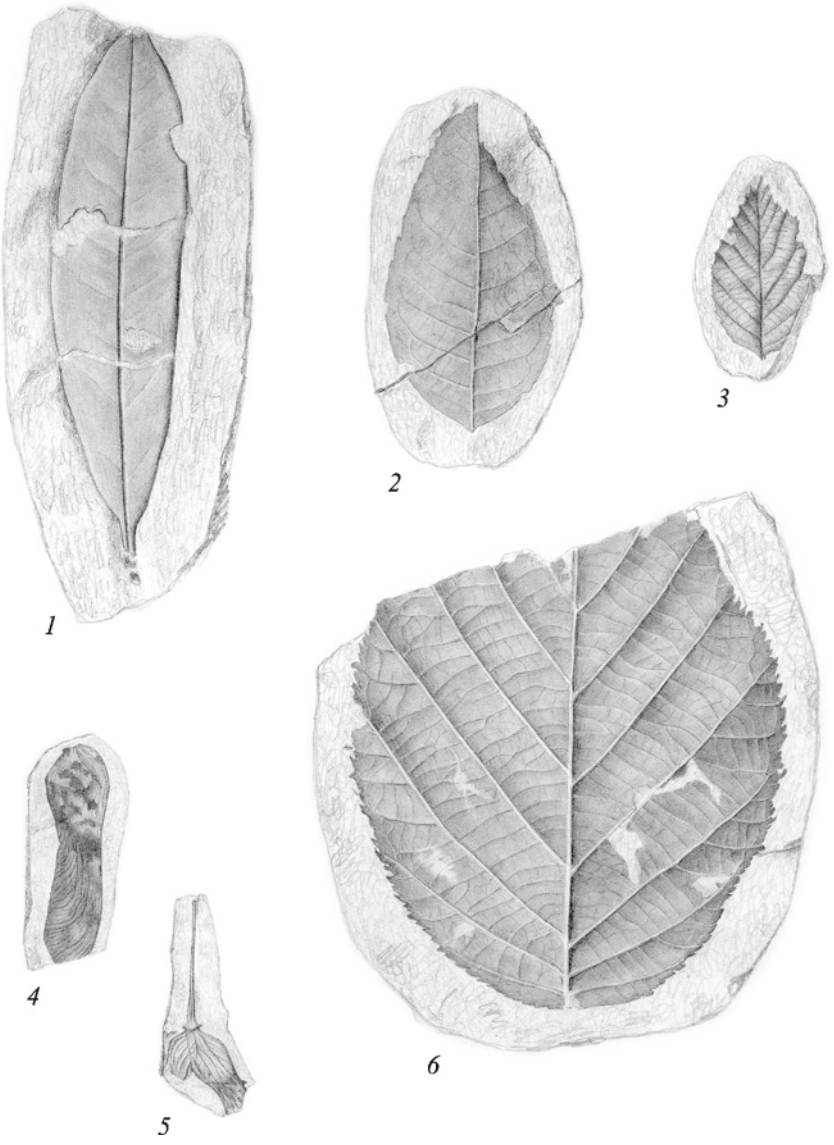



**Plate 14.30 (a)**

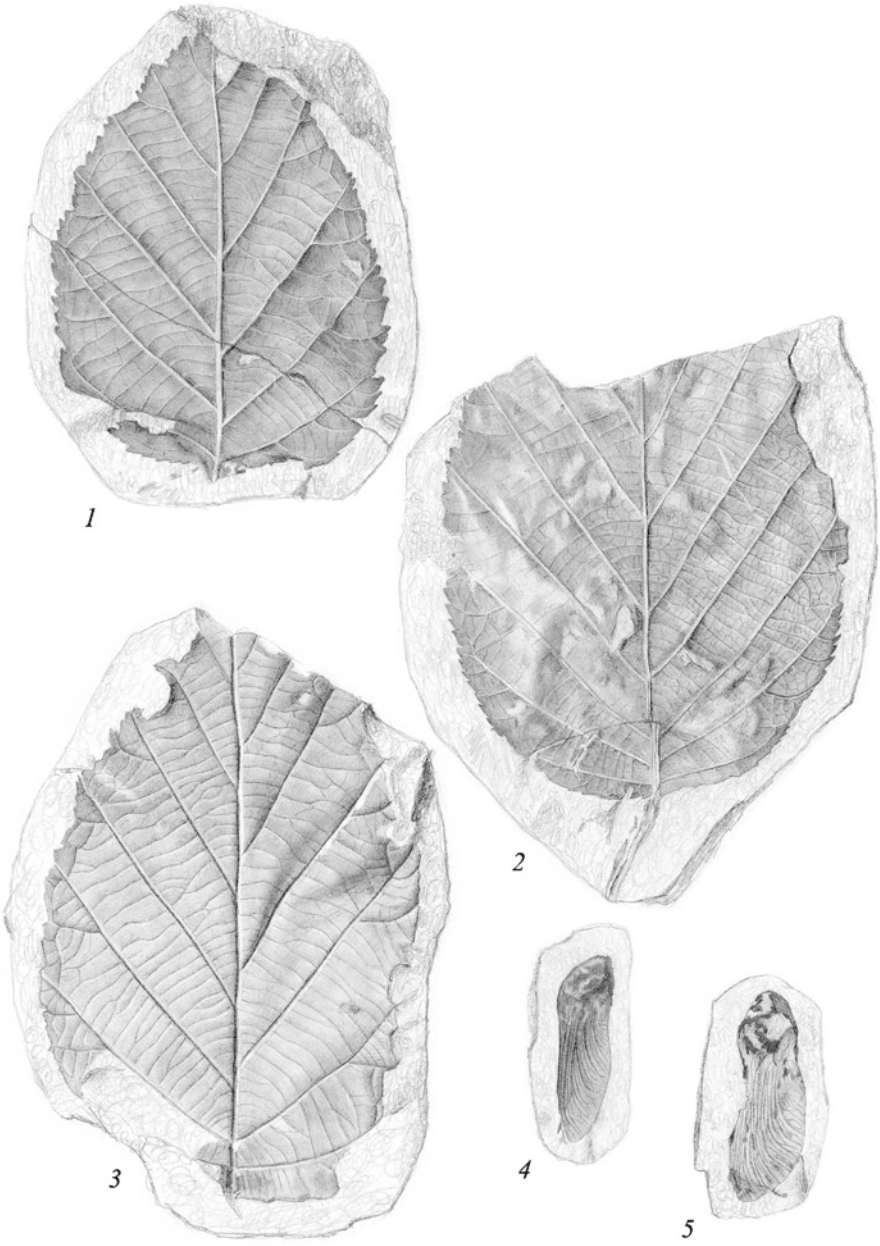



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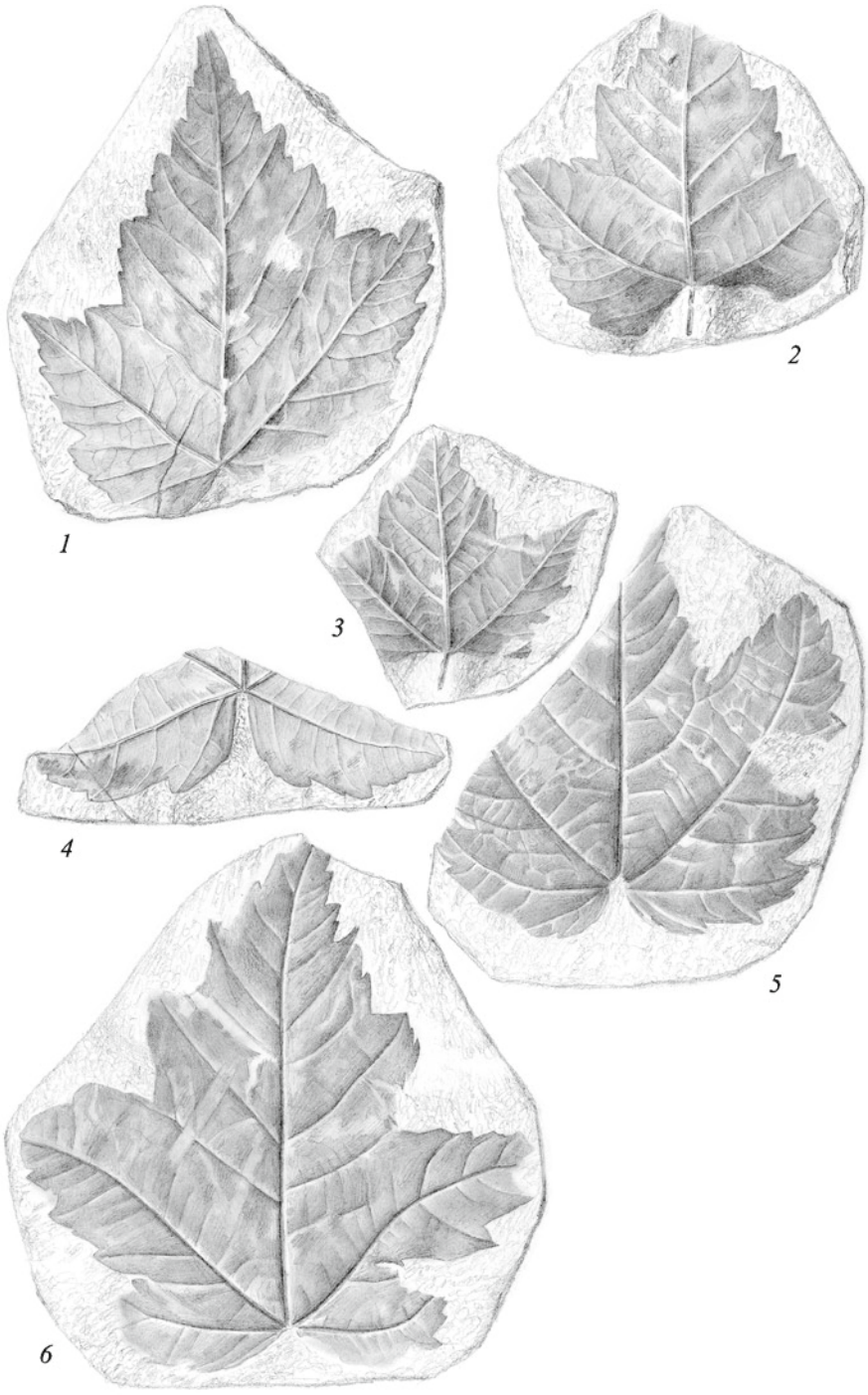



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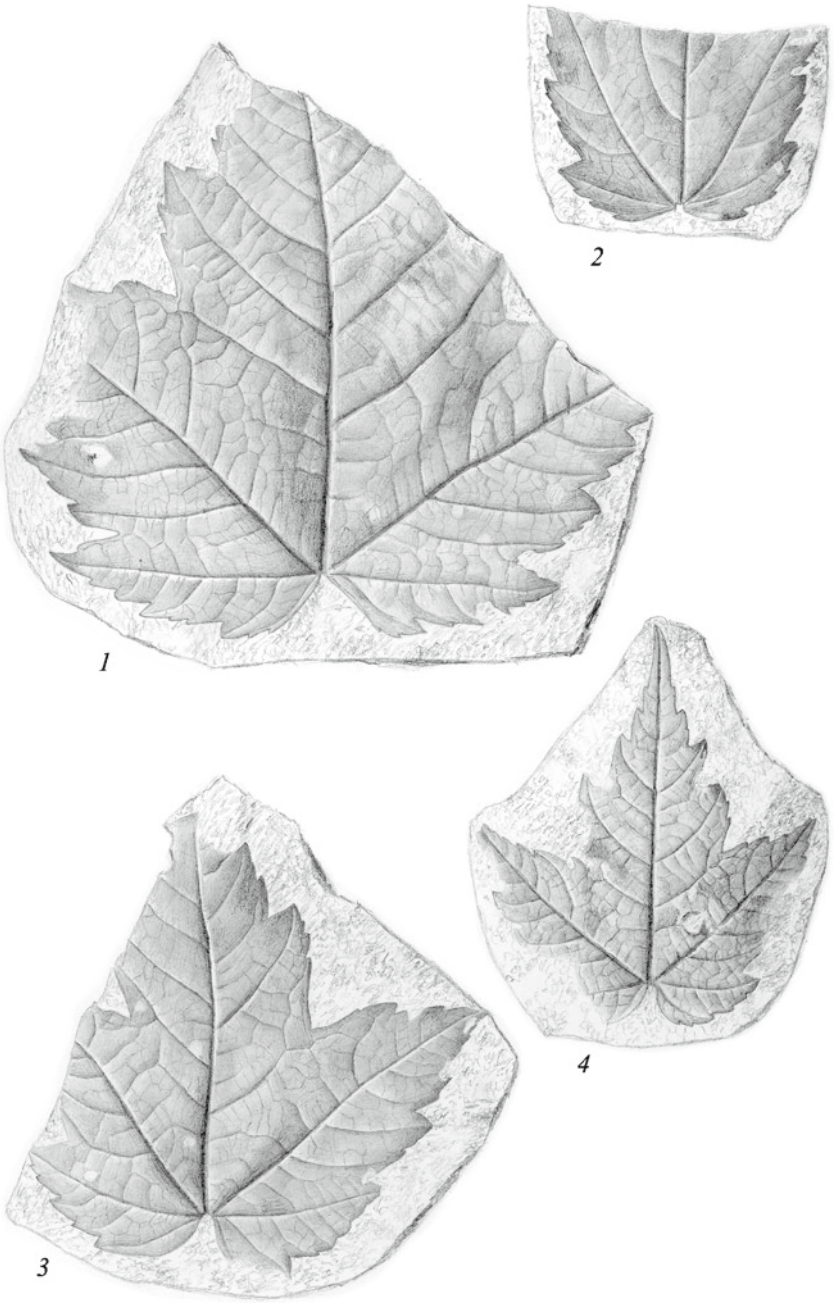



**Plate 14.32** (**a**)

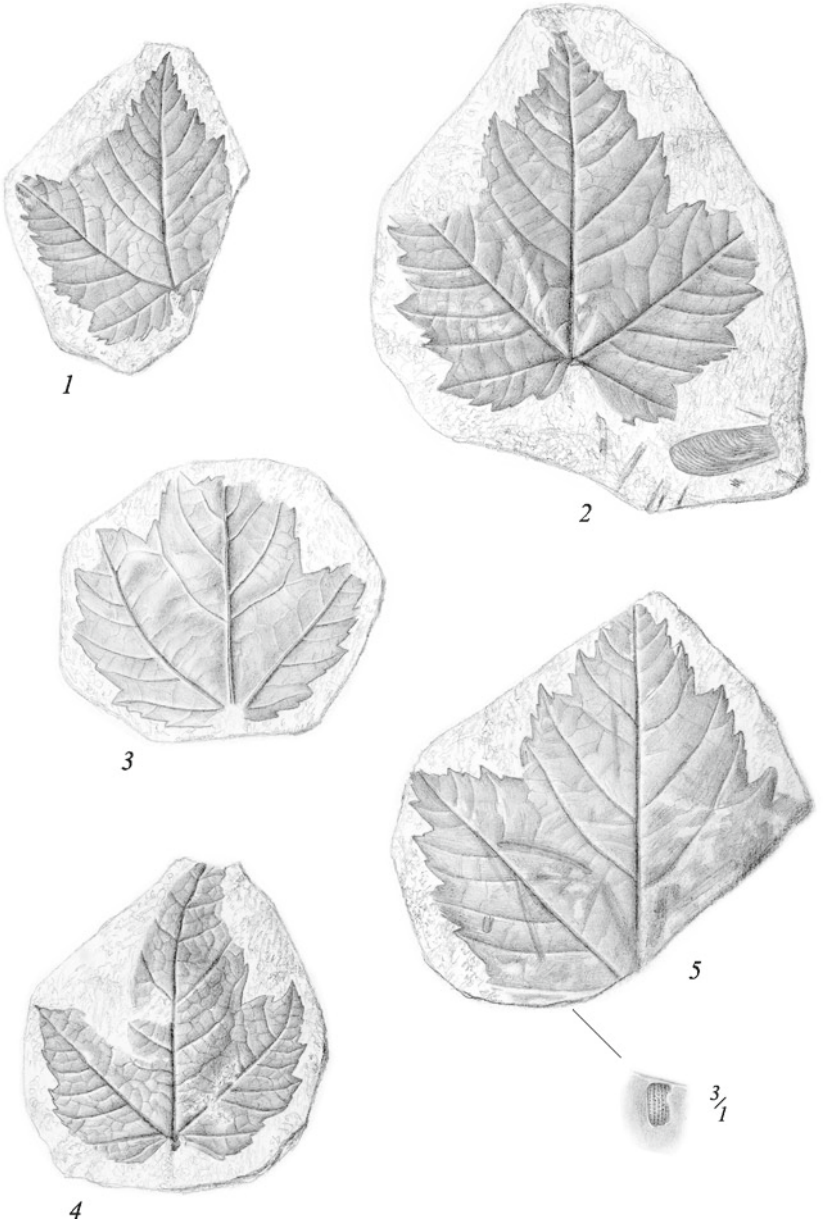



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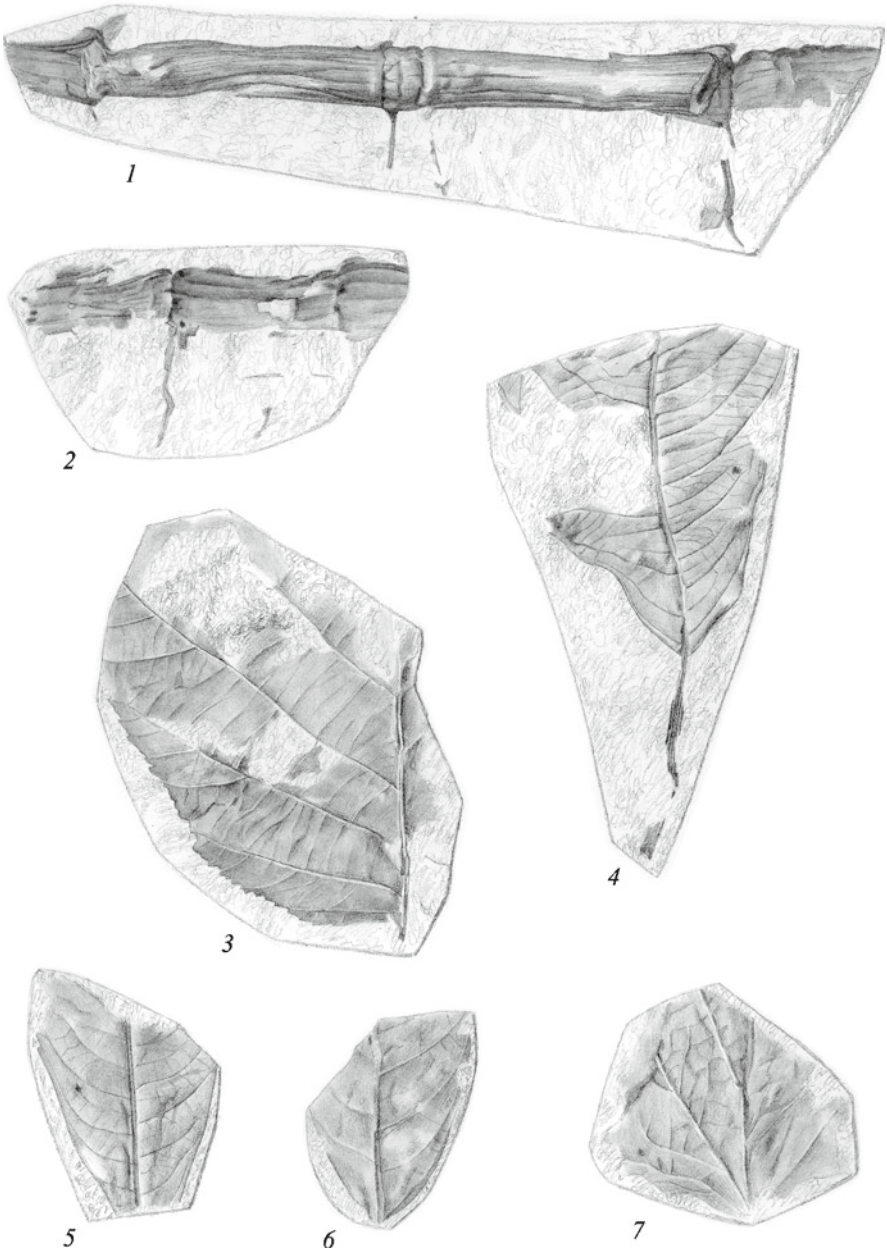



**Plate 14.33** (**a**)

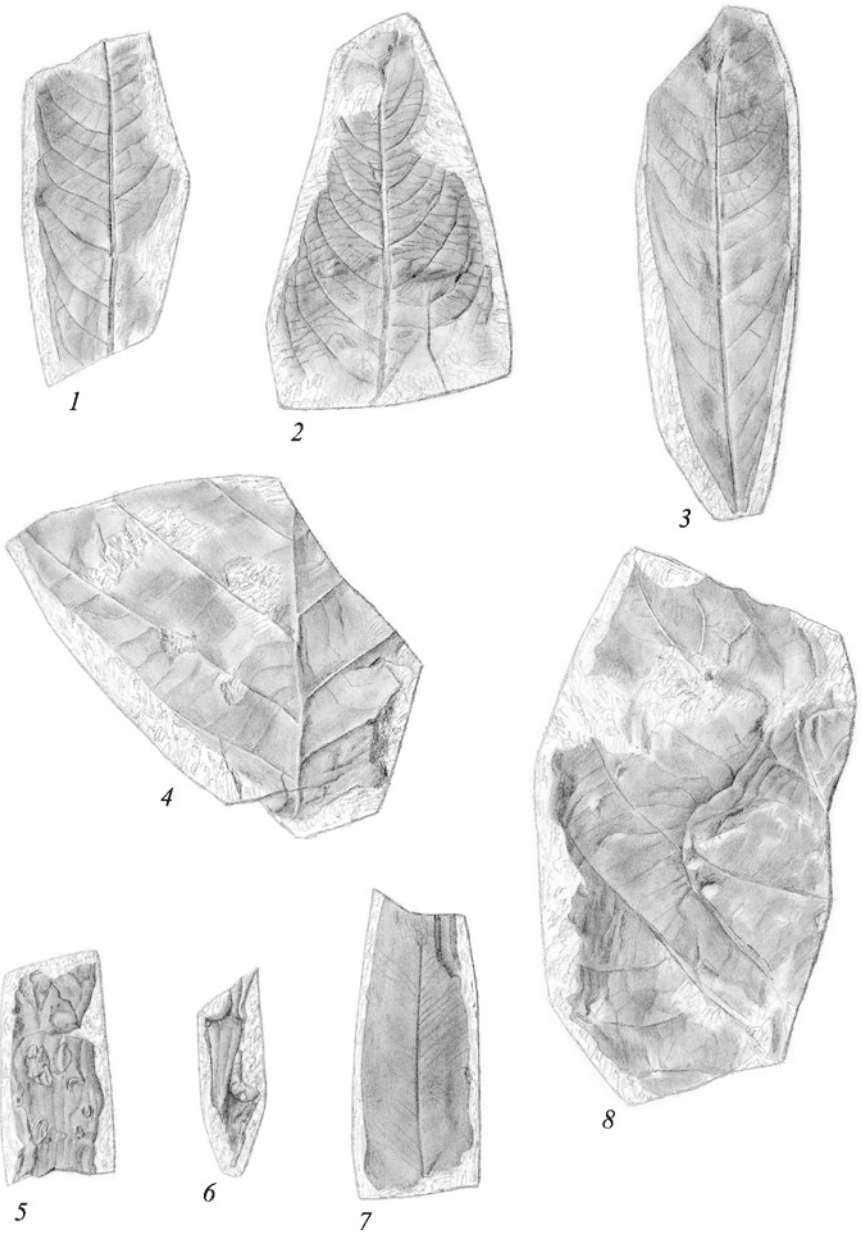



**Plate 14.33 (b)**




**Plate 14.34**




**Plate 14.35**




**Plate 14.36** (**a**)

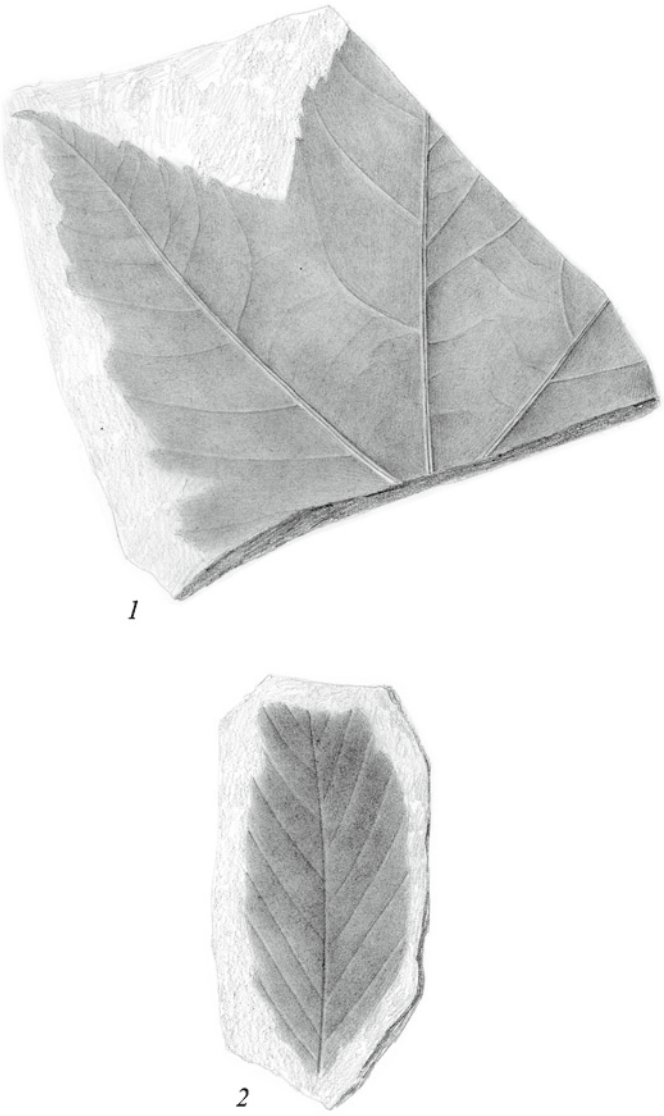



**Plate 14.36 (b)**




**Plate 14.37** (**a**)

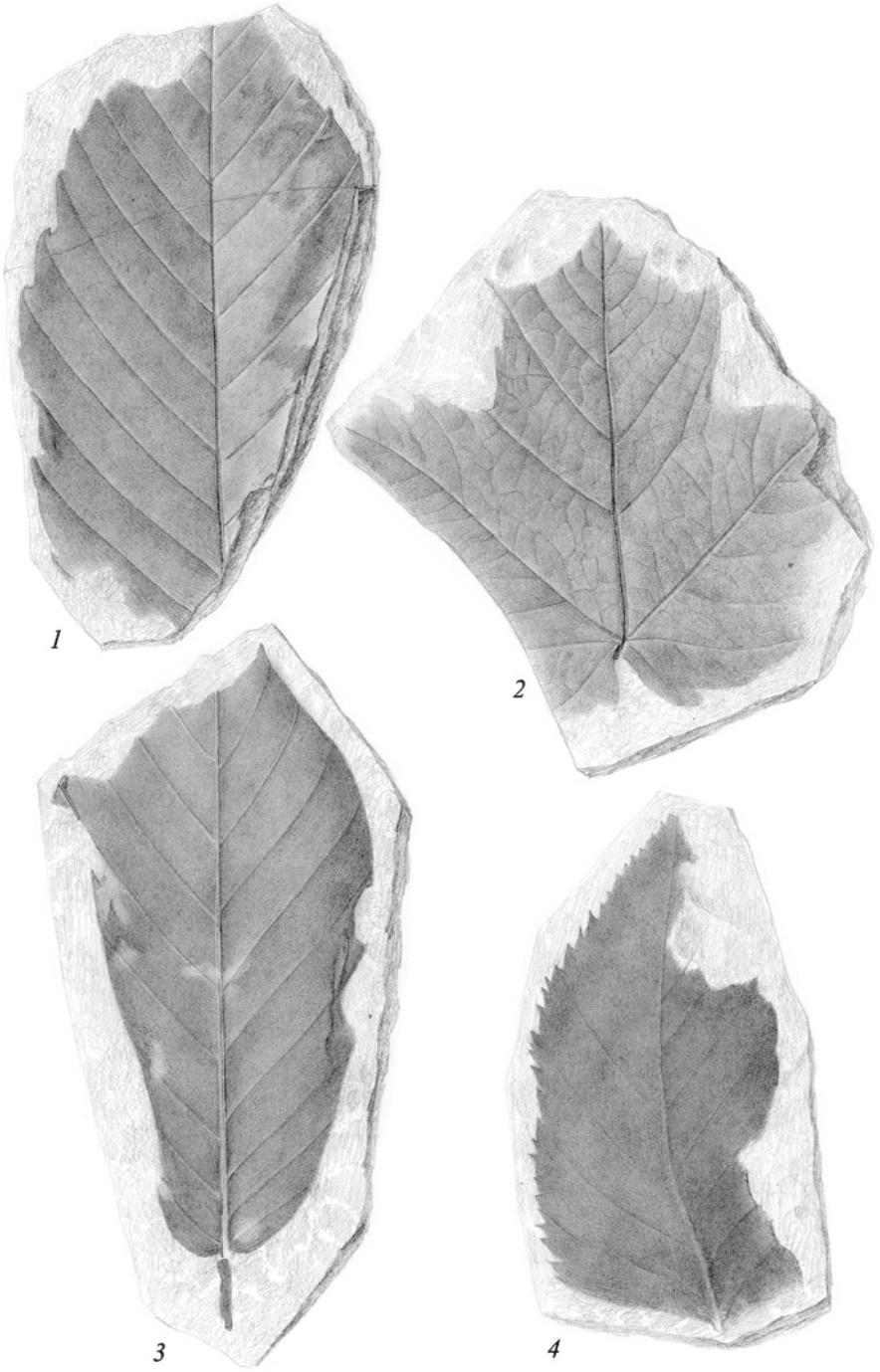



**Plate 14.37 (b)**

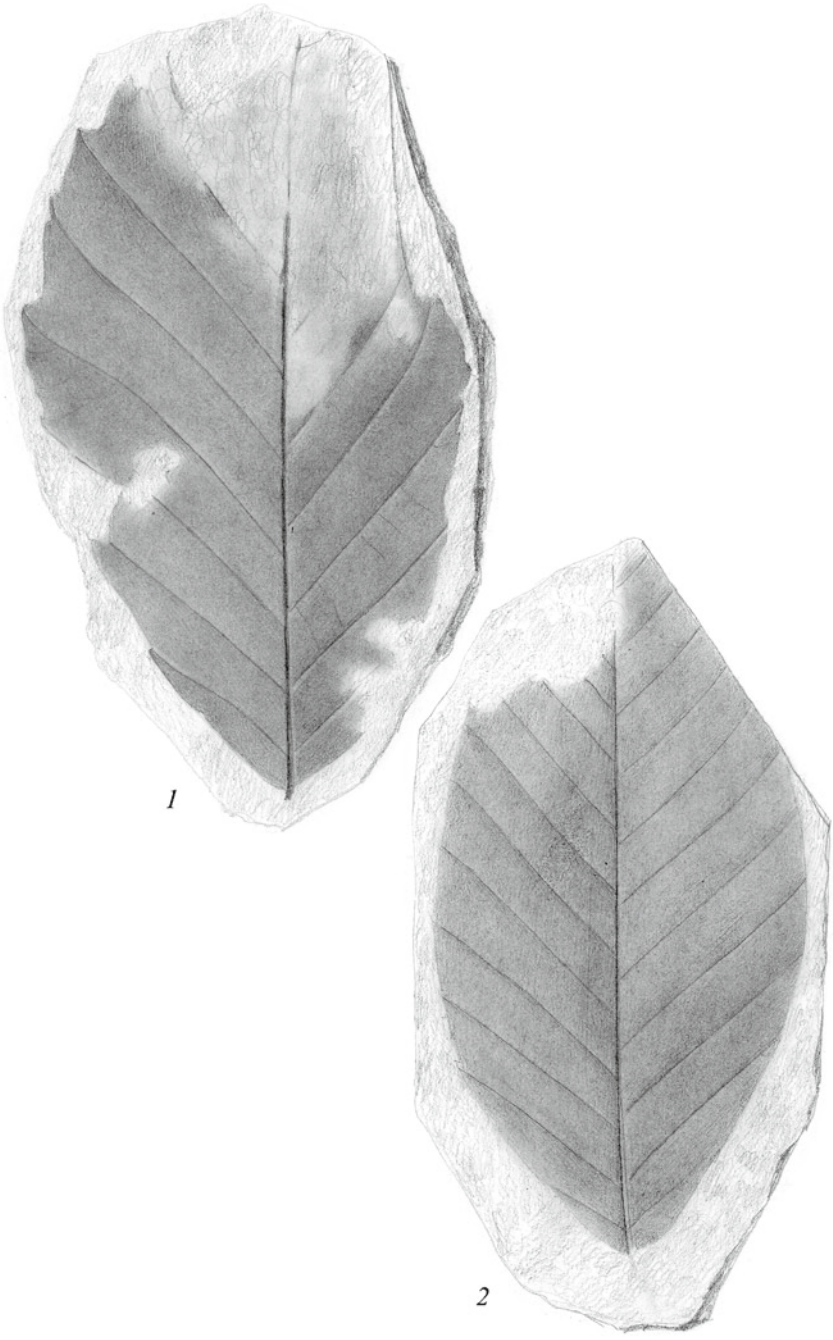



**Plate 14.38** (**a**)




**Plate 14.38** (**b**)

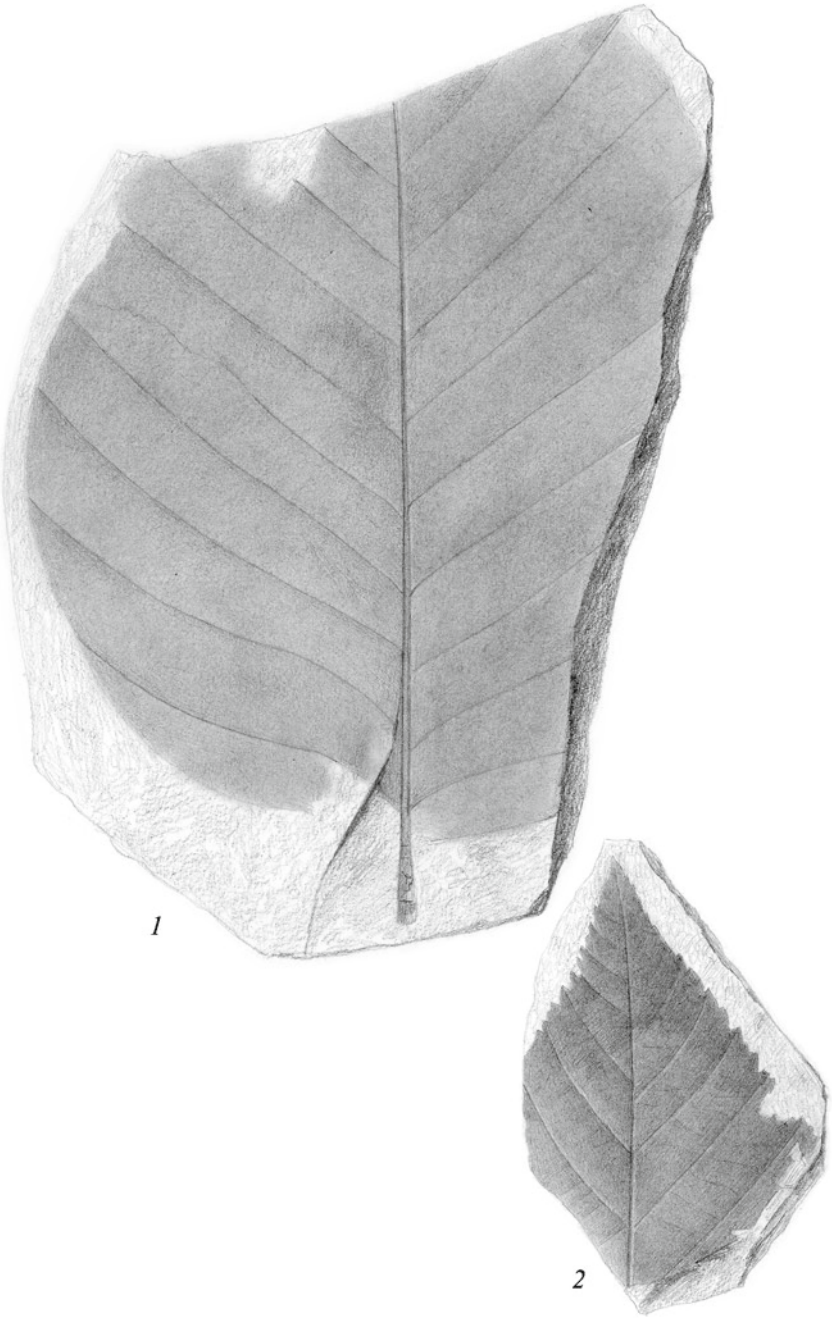



**Plate 14.39** (**a**)




**Plate 14.39 (b)**

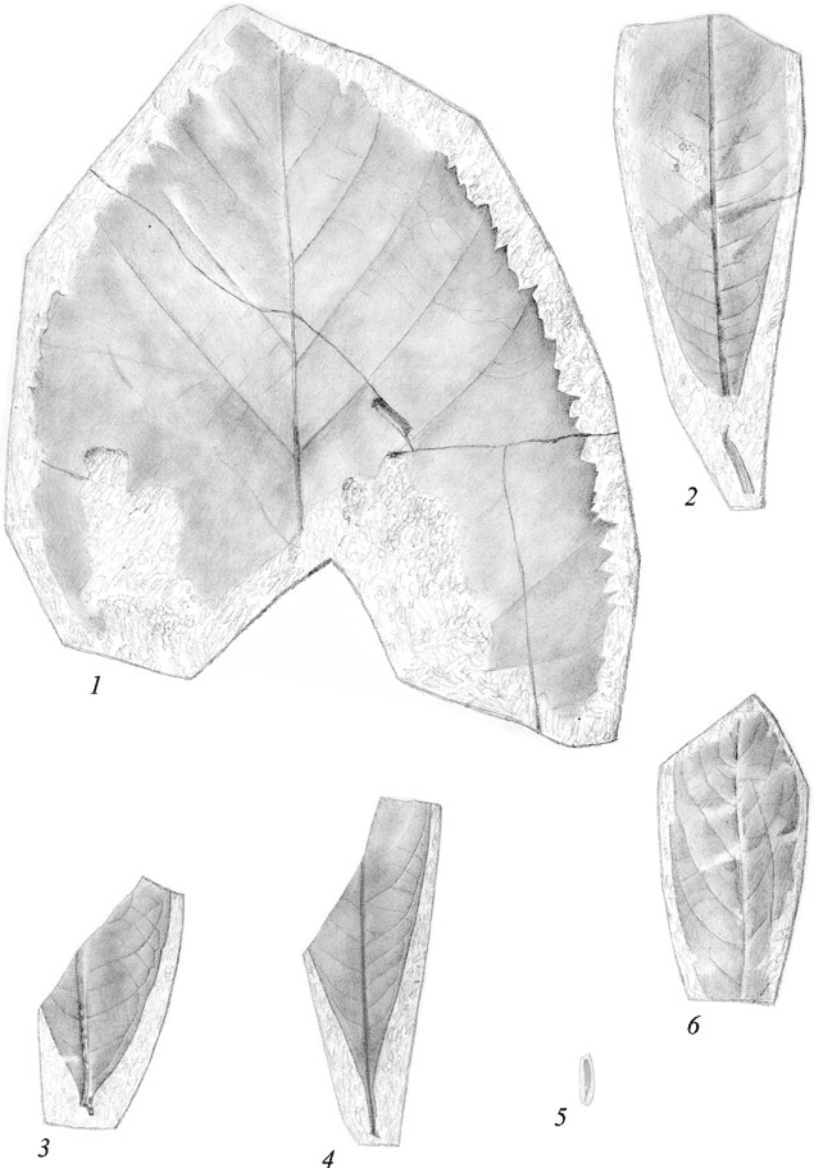



**Plate 14.40** (**a**)

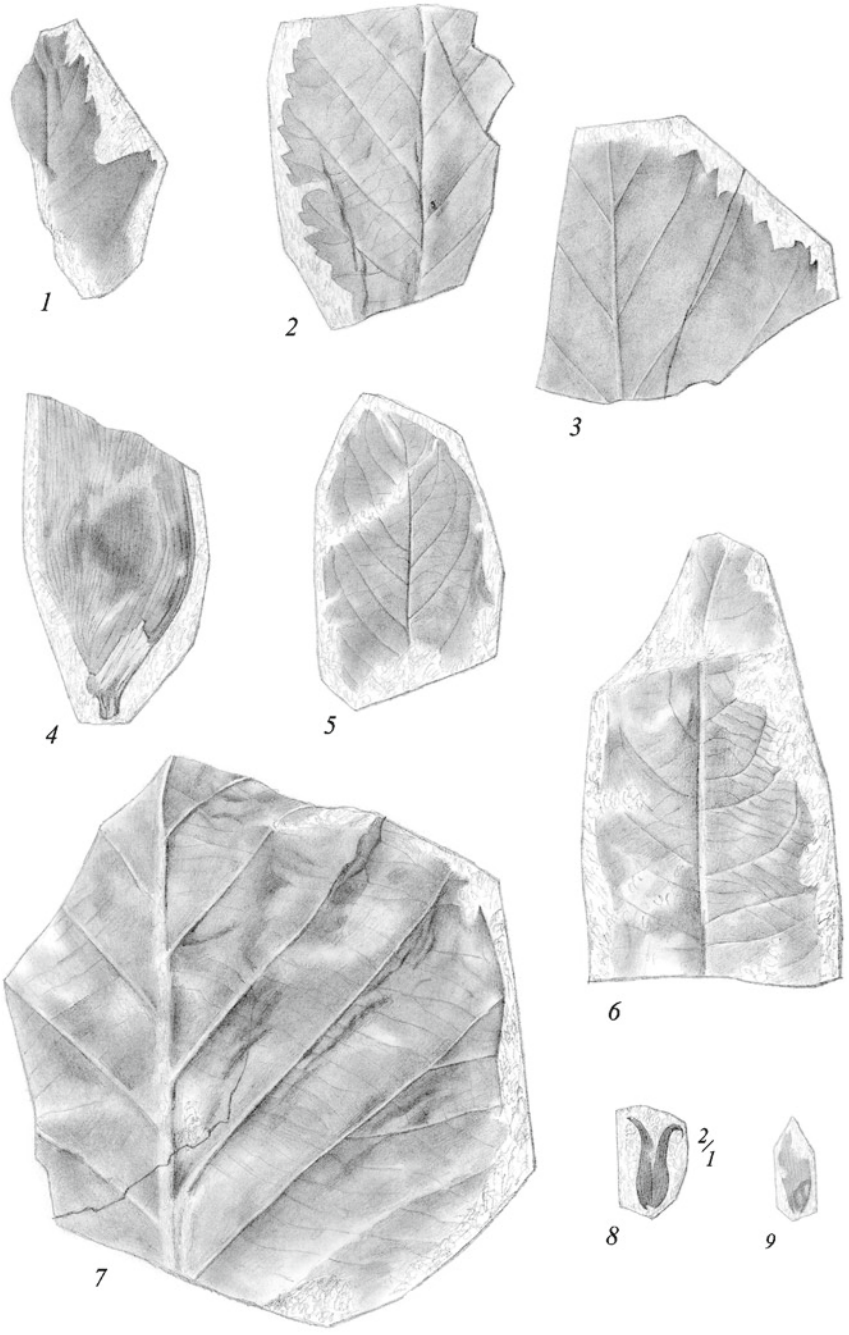



**Plate 14.40 (b)**

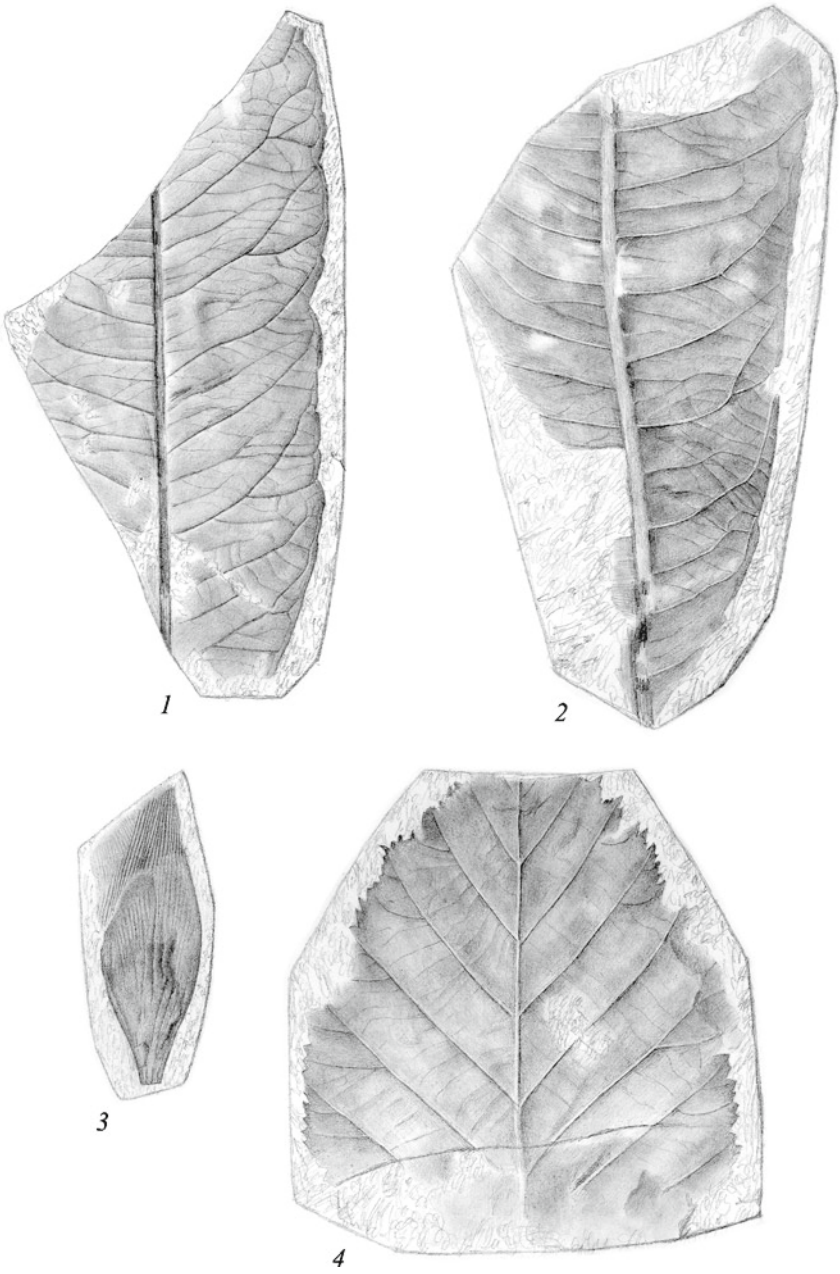



**Plate 14.41** (**a**)

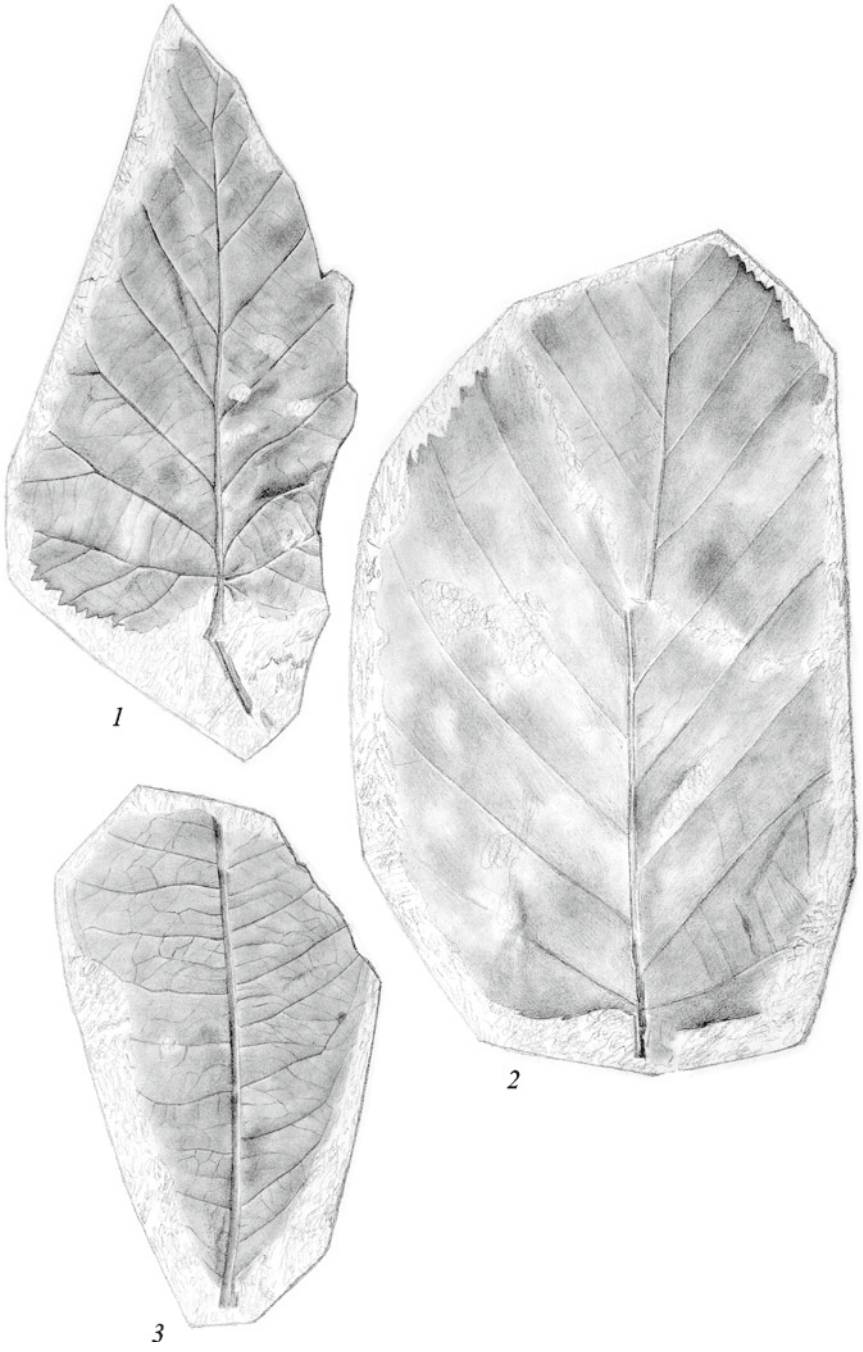



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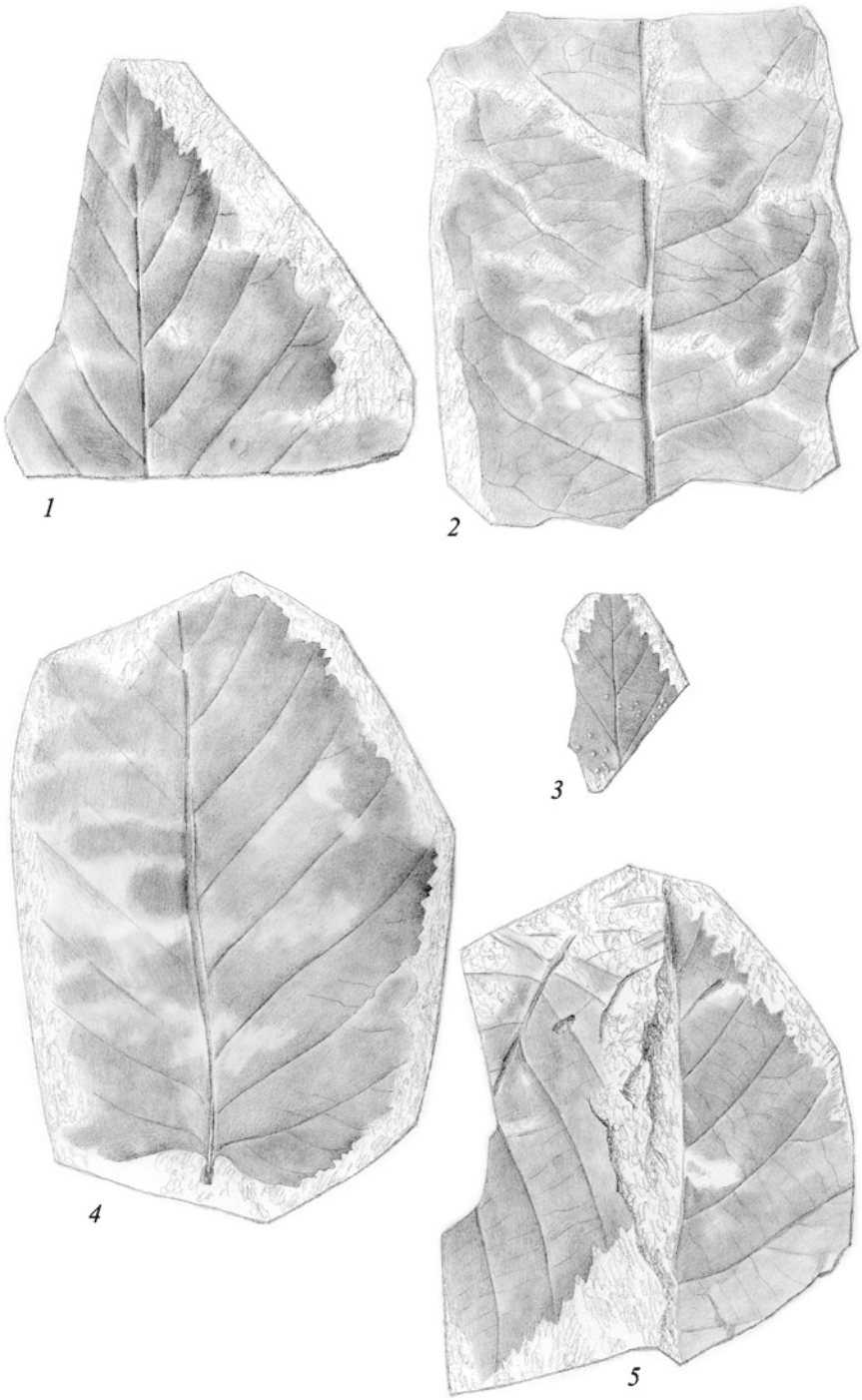



**Plate 14.42 (a)**

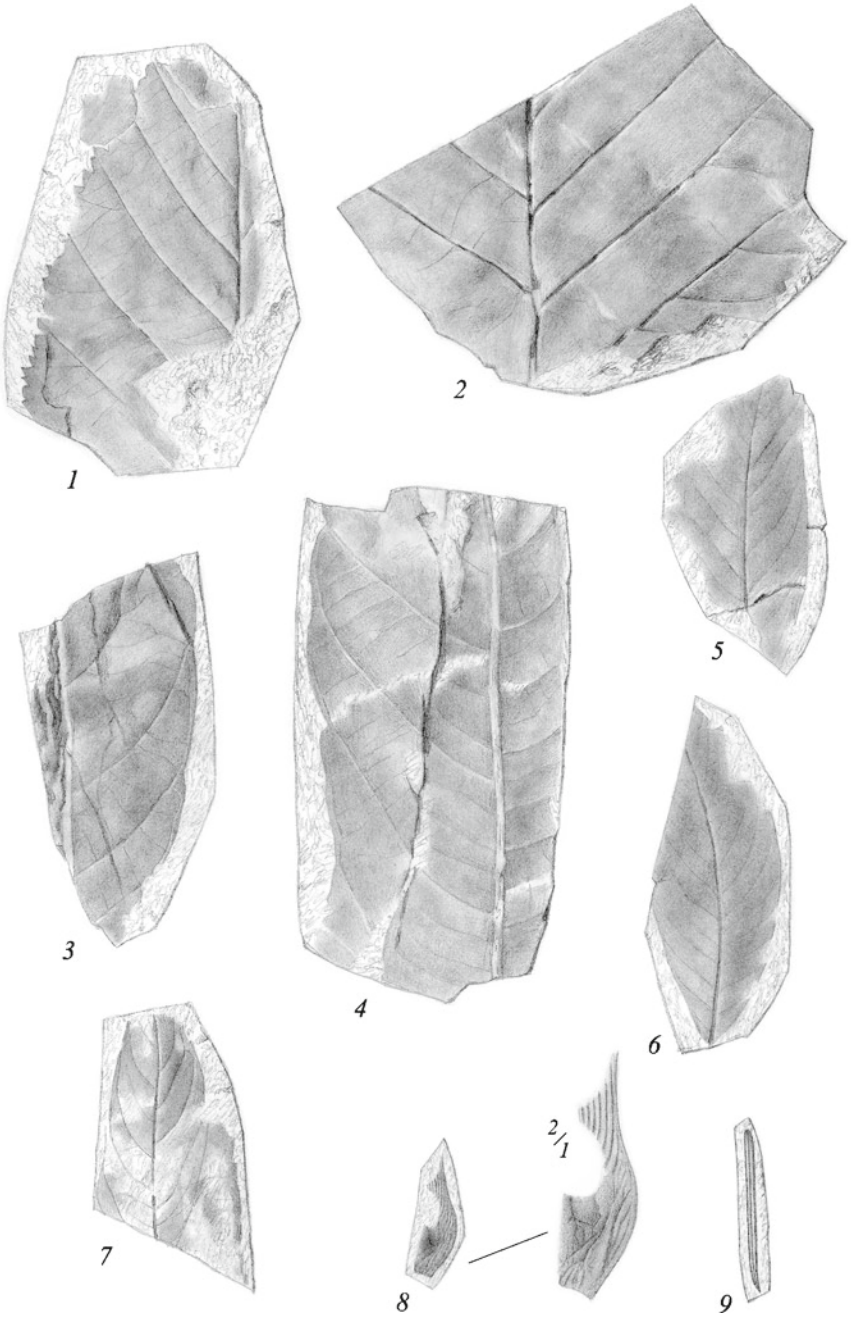



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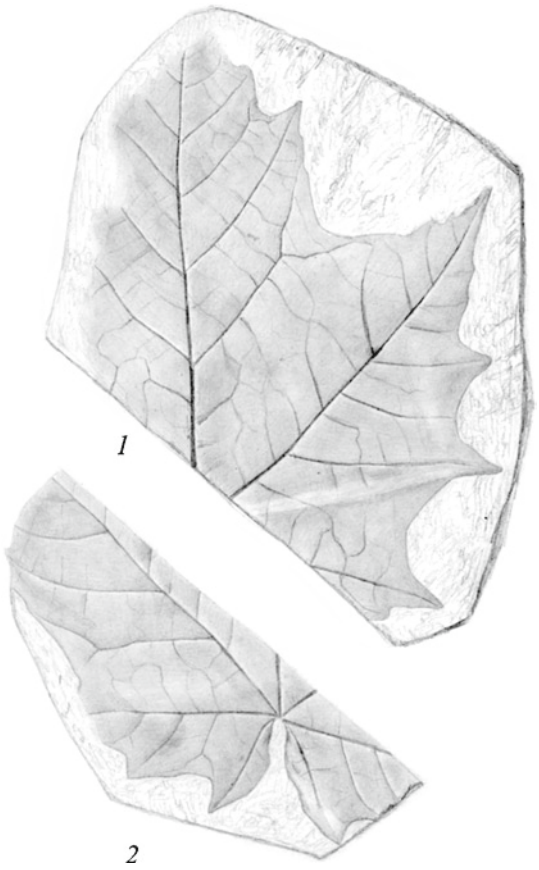



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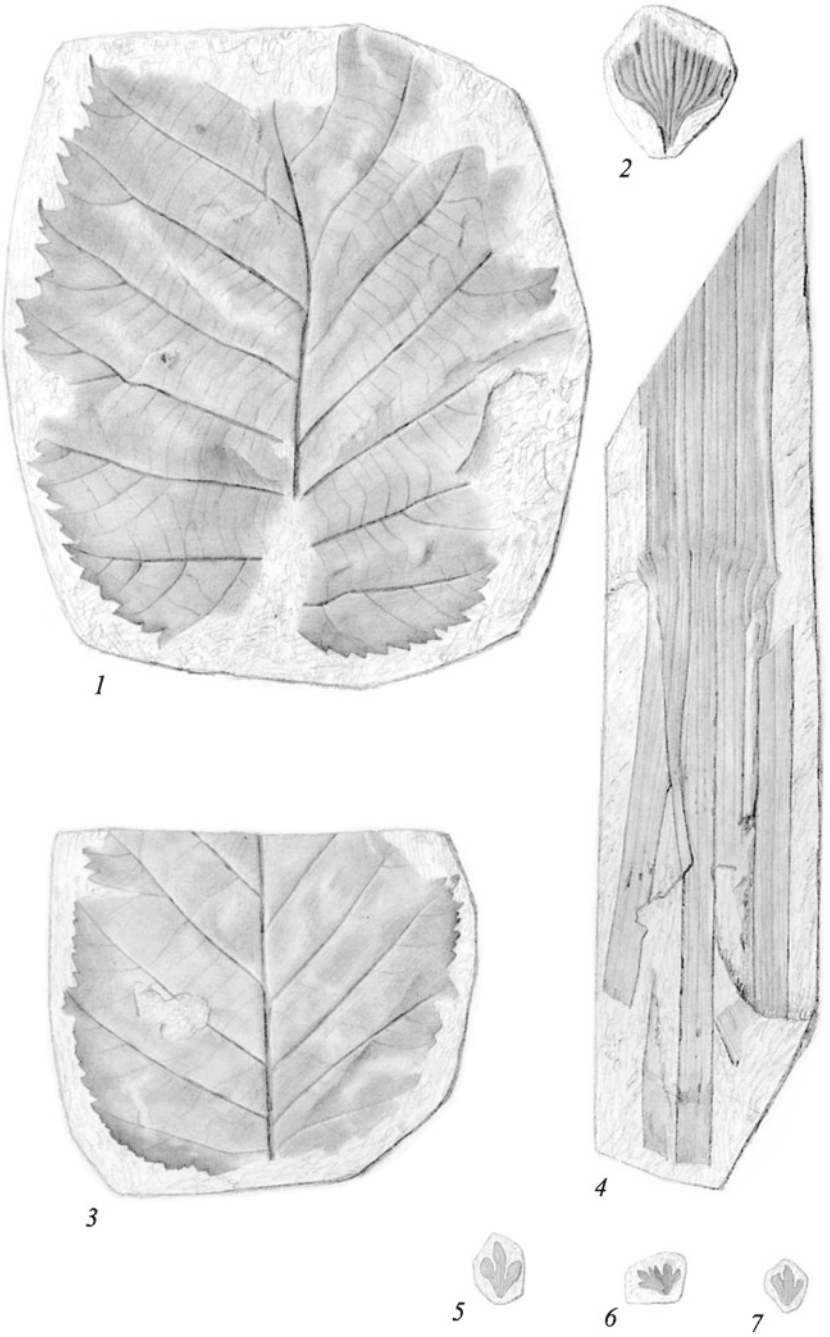



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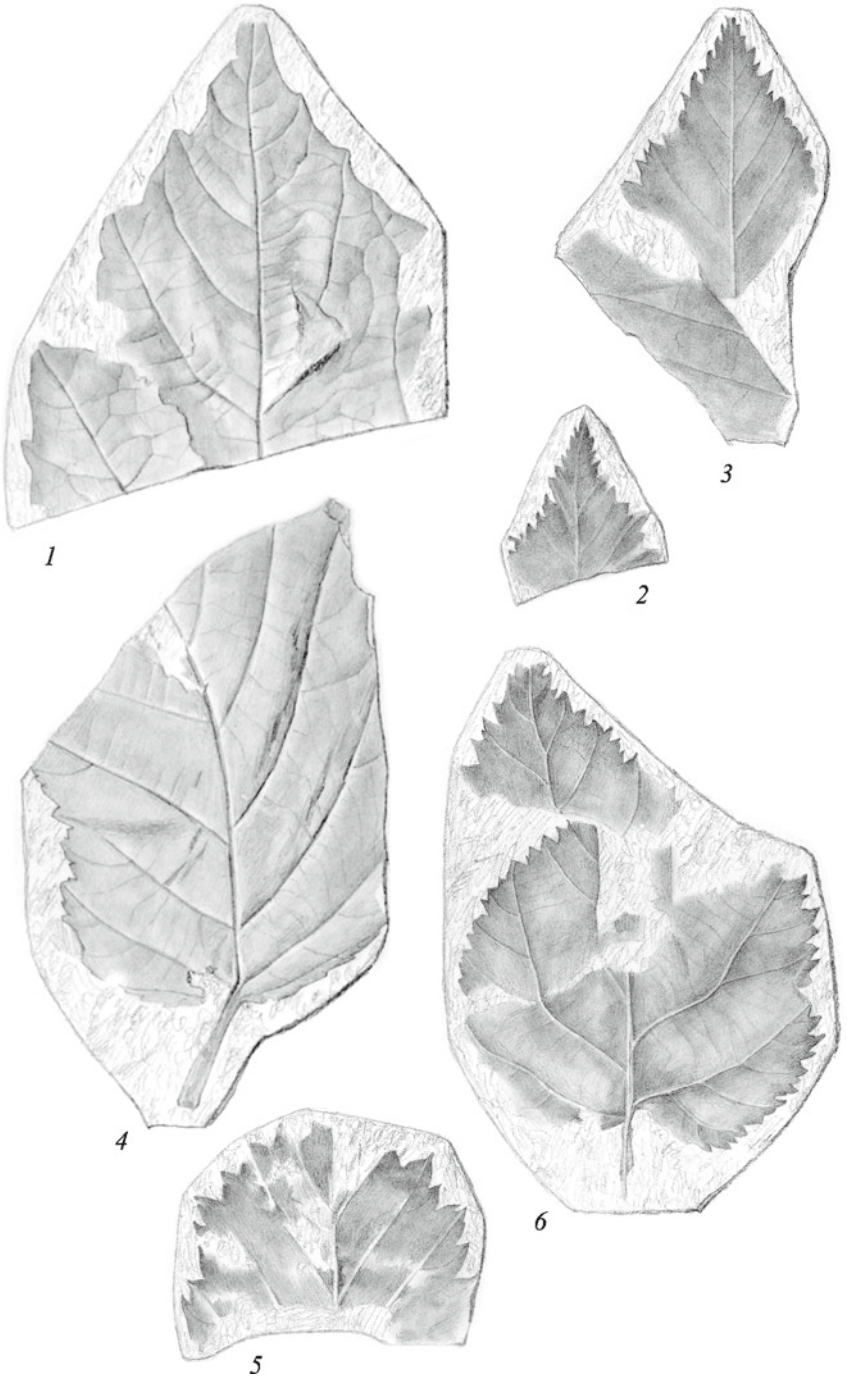



**Plate 14.44** (**a**)

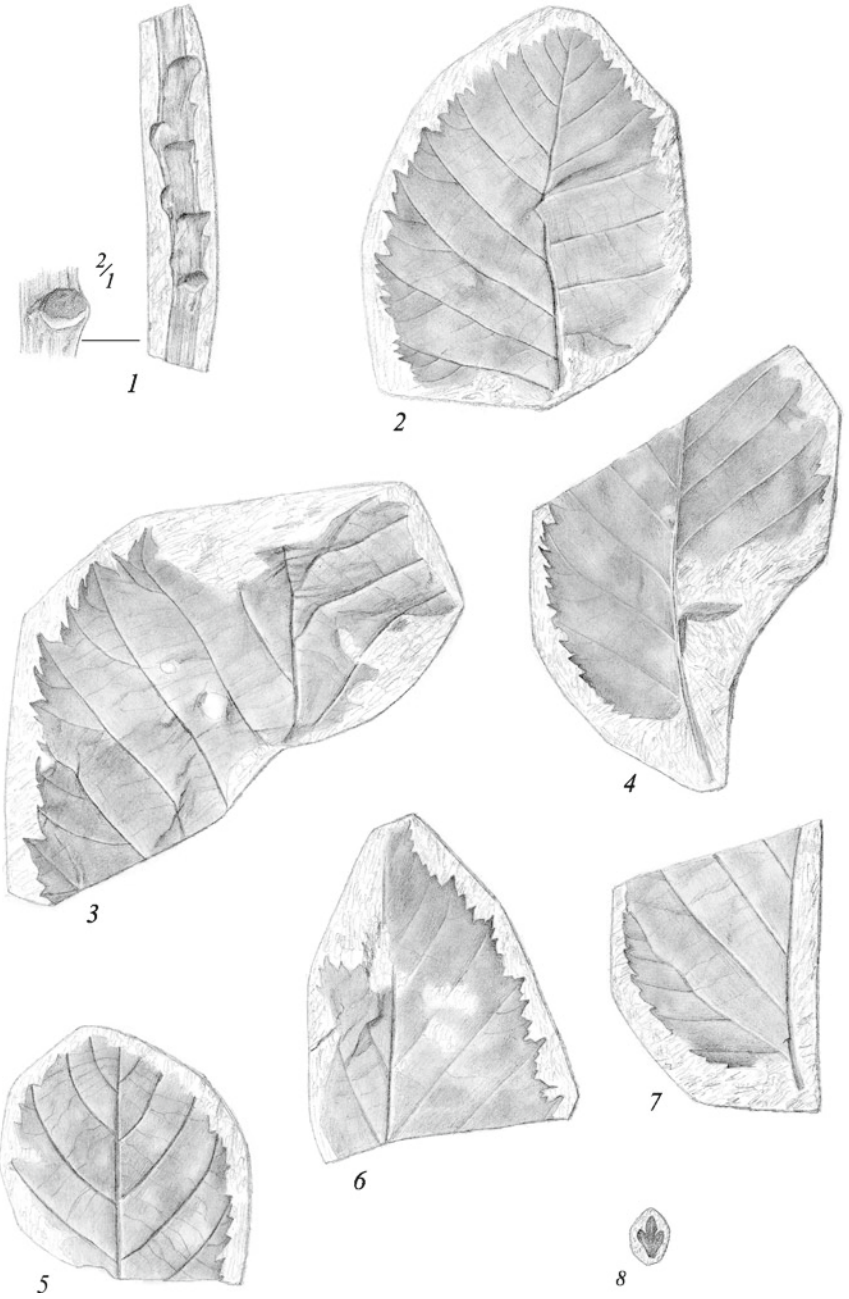



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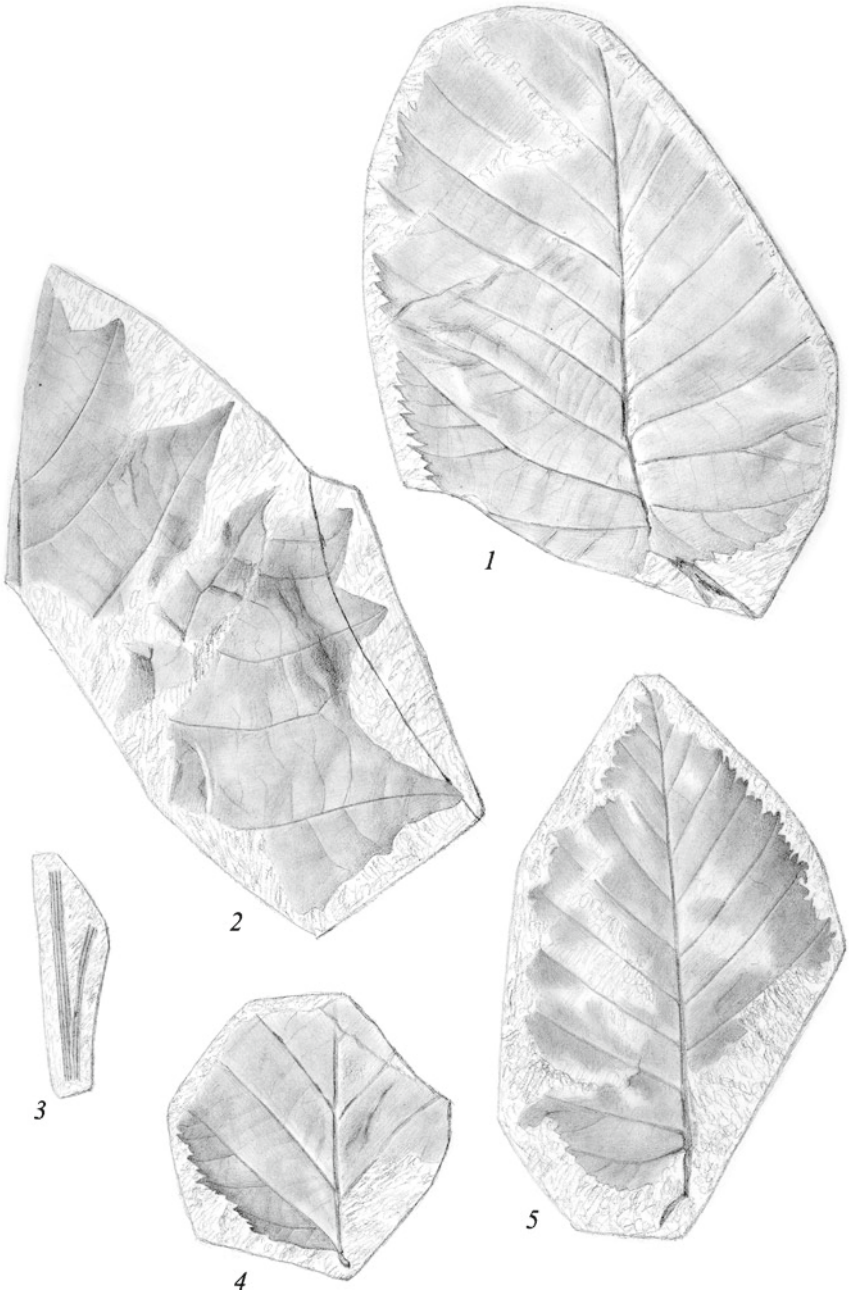



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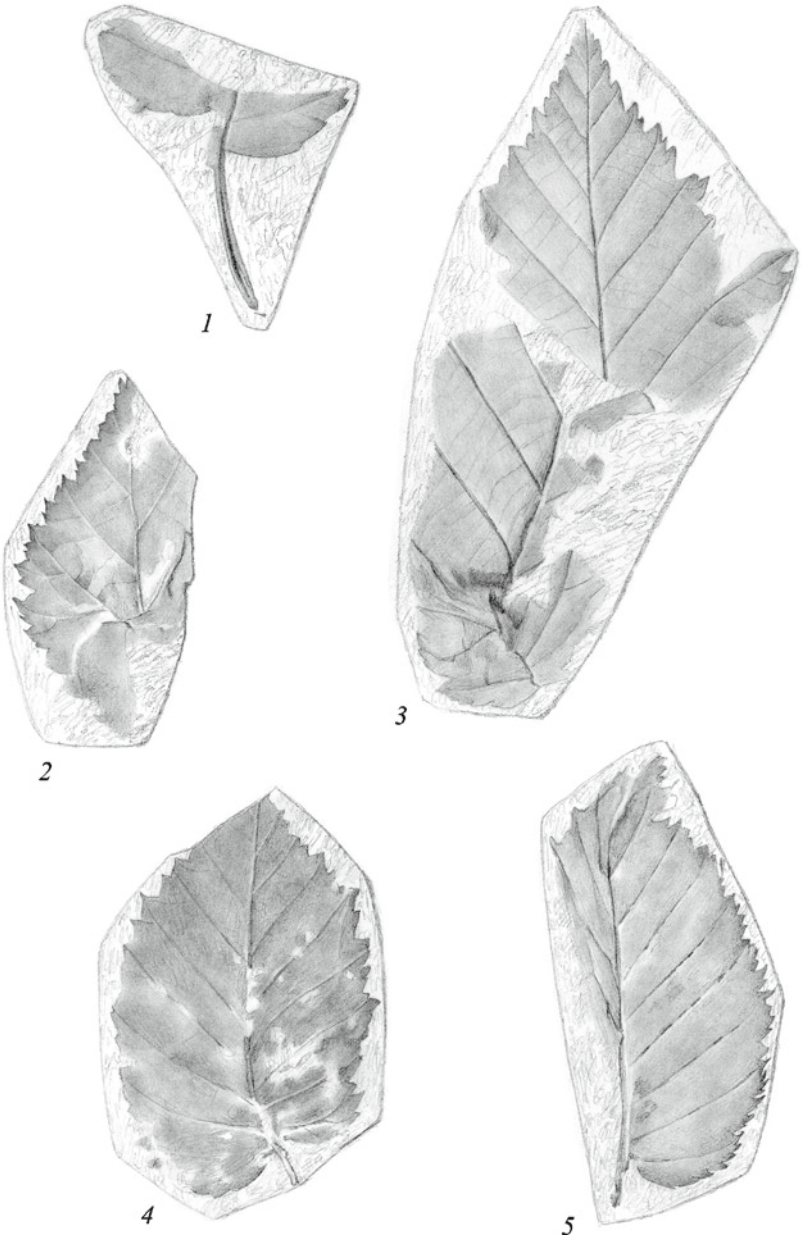



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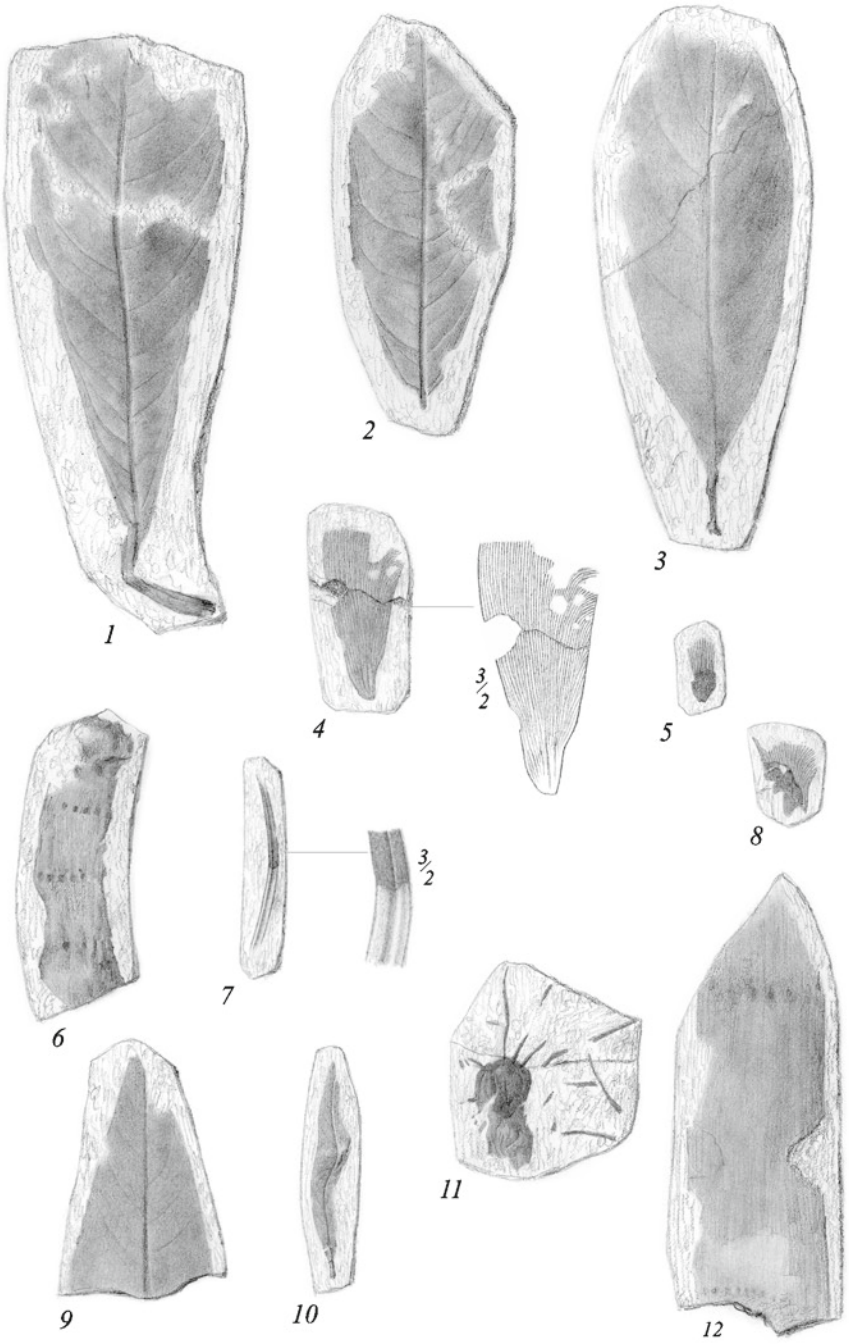



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